AN ABSTRACT OF THE THESIS OF

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Title: FACTORS AFFECTING THE ECOLOGY OF SMALL MAMMALS ON MALHEUR NATIONAL WILDLIFE REFUGE

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B. J. Verts

This study was conducted to examine factors in the ecology of small mammals on Malheur National Wildlife Refuge, Harney County, Oregon. Live-trapping and concurrent measurements of vegetative and edaphic habitat variables were conducted in four types of terrestrial plant communities between July 1973 and June 1975. Vegetative factors investigated were cover, patchiness of cover, foliage structure and succulence. Edaphic factors investigated were soil texture, depth, depth diversity, moisture content, strength and strength diversity. Linear regression analyses were used to examine correlations between habitat factors and the local distribution and abundance of small mammals.

Of 16 species of small mammals captured, deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*), Great Basin pocket mice (*Perognathus parvus*) and least chipmunks (*Eutamias minimus*) comprised 90.1 percent of the individuals. The

physiognomy of the vegetation was a factor in the distribution of rodent species other than deer mice. Pocket mice and chipmunks were restricted to the communities dominated by sagebrush (*Artemisia tridentata*) or greasewood (*Sarcobatus vermiculatus*). Population densities of pocket mice and chipmunks were significantly related to edaphic factors such as soil depth, texture and strength, that may have affected the construction and stability of burrows. Montane voles occurred only in marsh or grassland communities. Population densities of voles were directly correlated with the amount of cover and inversely correlated with its patchiness. Deer mice were the most common species encountered and occurred in all but the grassland communities. The density of this species was related to vegetative or edaphic factors only seasonally or in certain habitats, and few generalizations could be made.

Inverse numerical relationships were evident between chipmunks and deer mice in the sagebrush communities, and between chipmunks and pocket mice in the greasewood communities. These relationships were considered evidence of possible interspecific competition.

A 3-month lag-effect between vegetative succulence and the densities of deer mice, pocket mice and chipmunks was evident, but only in the one habitat type where each species attained its greatest abundance.

Factors Affecting the Ecology of Small Mammals on Malheur National Wildlife Refuge

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FACTORS AFFECTING THE ECOLOGY OF SMALL MAMMALS ON MALHEUR NATIONAL WILDLIFE REFUGE

INTRODUCTION

The determination of environmental factors which affect the distribution and abundance of a species is one of the fundamental aspects of animal ecology and small mammal biology.

The general habitat preferences of many species of small mammals have been documented by several generations of natural historians, and often can be attributed to food preferences and associated morphological adaptations (Baker 1971). Many other extrinsic factors affect populations of small mammals, including vegetation, soils, predation, competition and weather. Intrinsic factors, such as genetic and behavioral changes, also may be of significance (Krebs 1964:63-67). However, the quantitative relationships between many environmental factors and the distribution and abundance of small mammals usually are considerably less well known than their general habitat preferences. Therefore, the empirical determination of the effects of these factors on populations of small mammals remains a relevant objective of investigation.

This study was initiated to provide quantitative information concerning the effect of vegetative and edaphic factors on characteristics of the local distribution and abundance of small mammals inhabiting four community types on Malheur National Wildlife Refuge. In addition to the increased understanding of certain aspects of the ecology of small mammals, it was anticipated that the study would be useful to refuge personnel in the planning of physical changes on the area, so that impact on the small mammal fauna was consistent with management objectives.

DESCRIPTION OF THE AREA

Malheur National Wildlife Refuge is primarily a resting and breeding area for migratory waterfowl, and is located in the Harney Basin, Harney County, Oregon, between about 118.5° and 119.5° W. longitude and 42.7° and 43.4° N. latitude. The refuge was established in 1908 when 32,376 hectares (ha) (80,000 acres) were set aside as a Federal Bird Sanctuary. A major portion of the Blitzen Valley was added in 1935 and the Double-O Ranch area, in the lower Warm Springs Valley, was added in 1941, to form the present T-shaped refuge (Fig. 1) of approximately 73,251 ha (181,000 acres) (United States Department of the Interior 1974). Gabrielson (1943) provided a brief general history of the refuge and a description of some of the early conditions that existed there.

The Harney Basin encompasses portions of the high lava plains and the basin-range physiographic divisions of Oregon (Dicken 1955). The lava plains area is a relatively undeformed region of lava flows, lava buttes, cinder cones, tuffs and alluvium of Pliocene and Pleistocene origin. The basin-range area is characterized by fault block mountains oriented north-south, and basins of internal drainage (Baldwin 1959).

The refuge is at an elevation of approximately 1,250 meters (m) (4,100 feet). It is characterized by dry summers with temperatures

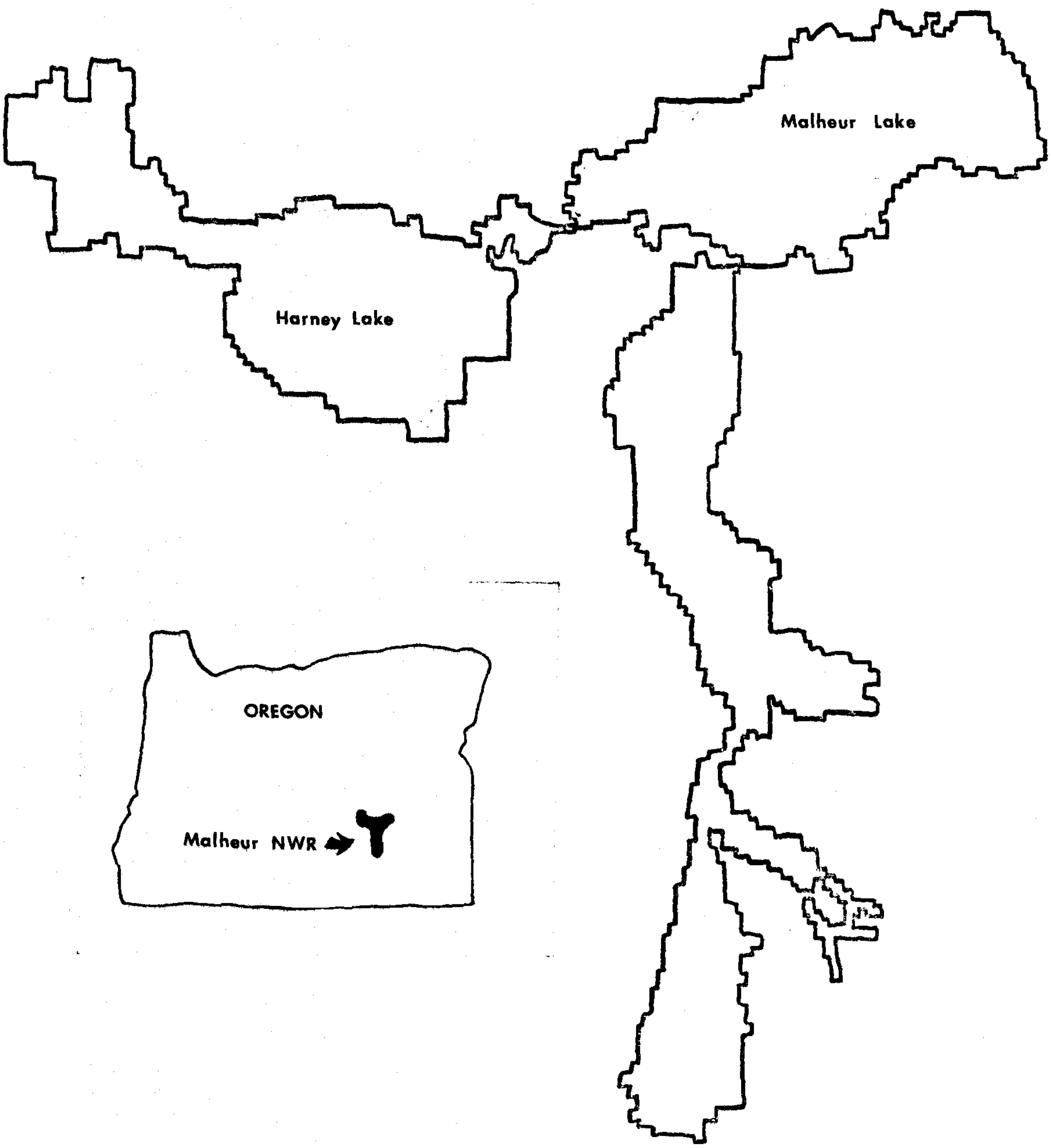


Figure 1. Outline map of Malheur National Wildlife Refuge, Harney County, Oregon. Inset shows location of the refuge in southeast Oregon.

rarely exceeding 32.2°C (90°F) and cold winters with average temperatures below -6.6°C (20°F). The average annual precipitation is 22.9 cm (9.0 in), much of which occurs as snowfall (Meteorology Committee, Pacific Northwest River Basins Commition 1969).

Major drainages into the Harney Basin and the refuge are the Silvies River and Silver Creek flowing from the Blue Mountains to the north, and the Donner Und Blitzen River flowing from the Steens Mountain highlands to the southeast (Lindsey et al. 1969). The Silvies River drains approximately 3,496 square kilometers (km^2) (1,350 sq. miles) and flows into the north side of Malheur Lake, while Silver Creek discharges into Harney Lake. The Donner Und Blitzen River drains approximately 2,590 km^2 (1,000 sq. miles) and empties into the southern portion of Malheur Lake, providing the major source of water for the refuge (USDI 1957).

Harney Lake, a shallow, alkaline lake practically devoid of vegetation, is the lowest part of the drainage and usually covers about 12,141 ha (30,000 acres). Malheur Lake, a shallow, alkaline marsh of about 20,235 ha (50,000 acres) supports dense, interspersed stands of emergent vegetation including hardstem bulrush (Scirpus acutus), cattail (Typha latifolia) and baltic rush (Juncus balticus) as well as submerged aquatic plants, particularly sago pondweed (Potamogeton pectinatus), horned pondweed (Zannichellia palustris), water milfoil (Myriaphyllum exalbescens) and others (Duebbert 1969). Both lakes vary in the size of their surface areas, depending on the availability of water, and both may become dry during extended periods of drought.

Besides Harney and Malheur Lakes, a high proportion of the refuge consists of valley wetlands vegetated primarily by rushes, sedges (Carex sp.) and submerged and emergent wetland flora. Drainage is usually poor on these wet, alluvial soils (Lindsey et al. 1969), and approximately 8,094 ha (20,000 acres) of this bottomland is under cultivation (Rouse, unpublished data). Rimrock areas above the valley floor support mainly big sagebrush (Artemisia tridentata), greasewood (Sarcobatus vermiculatus) and grasses, principally the exotic annual, cheatgrass (Bromus tectorum).

The earliest recorded faunal information from what is now the present site of the refuge was that of Peter Skene Ogden, who led a party of fur trappers to the area in 1826 (Elliott 1910). In the early 1900's, various members of the Biological Survey collected bird and mammal specimens in the Harney Basin. In 1906, Vernon Bailey collected data on the past occurrence of mountain sheep (Ovis canadensis) in the Steens Mountain area (Olterman and Verts 1972). In the 1930's, the remains of bison (Bison bison) and grizzly bear (Ursus arctos) that once inhabited the area were picked from the dry bed of Malheur Lake (Bailey 1936). Small areas of the eastern portion of the refuge were sampled for vertebrate fauna in the early 1950's (Hansen 1956). The latest list of mammalian species known to inhabit the refuge contained 53 entries (USDI 1975).

METHODS AND MATERIALS

Eighteen study plots were established on the refuge among the four predominant types of terrestrial plant communities. Five plots were established in both sagebrush and greasewood areas and four plots were established in both marsh and grassland communities (Table A). Areas designated as marsh were characterized by habitat factors that generally conformed to the "inland shallow fresh marsh" category of Shaw and Fredine (1956:21). Areas designated as grassland conformed to their "inland fresh meadow" category. Locations of study plots were selected at random from among areas in each community that met the following criteria: 1) relative vegetative homogeneity; 2) within 0.8 km of a paved, gravel or dry weather road; and 3) large enough to encompass the trapping grid plus the border area. Live-trapping on all plots was conducted once during 1973, twice in 1974 and once in 1975. Each trapping period roughly corresponded seasonally to either spring (April through May), summer (June through August) or fall (September through November). An exception was the 1973 trapping period (July through September). Traps were not placed on plots that were flooded. Vegetative and edaphic parameters were measured on each study plot concurrently with the trapping periods.

Although no quantitative analysis of the effect of predation on small mammal populations was attempted, numerous species of potential predators were known to inhabit the refuge during the study period. Predatory species that may have utilized the small mammal fauna to varying extents are listed in Table B.

Small Mammals

Trapping Procedures

Trapping grids consisted of Sherman live-traps placed in lines 90.0 m in length. Lines consisted of seven stations spaced at 15.0-m intervals with one trap at each station. Seven such parallel lines were placed at 15.0 m intervals to form a square grid of 49 traps encompassing an area of 1.1 ha (2.7 acres). This area included a border of 0.3 ha (0.7 acres) from which it was assumed animals would be captured.

Traps were operated for 10 consecutive days, except during 1973 when grids were operated for 3- or 4-day periods. Each trap was baited with rolled oats, and contained Dacron batting for nesting material. Traps were covered with aluminum shields and, when possible, were placed in the shadow of vegetation to minimize exposure of animals to heat. Animals were removed from traps as soon after dawn as possible.

Trapped animals were individually marked by toe-clipping following the procedure outlined by Taber and Cowan (1971), and released at their respective points of capture. The species, sex, reproductive condition, age class, weight and trap locality of each captured animal were recorded.

Males were considered reproductively active if their testes were descended. Females were considered pregnant if their abdomens were visibly swollen or developing young were detected by palpatation. A litter was considered to be suckling if the fur was absent from around the teats or if mammae were large and protruding.

At least at the initial capture each trapping period, each animal was weighed to the nearest gram using a portable spring scale. Individuals were classified as juvenile or adult on the basis of body size, weight or pelage color. Individuals were considered juveniles if their body weight was less than 75 percent of the mean adult weight of the species reported in previous studies (Bailey 1936, Hall 1946, Asdell 1964, Layne 1968). Pelage color of deer mice (Peromyscus maniculatus) also was used to determine age class. Deer mice were considered juveniles, regardless of weight, if they had grey pelage or had not completed their post-juvenal developmental molt (Layne 1968).

Estimation of Density

The average densities of each species ($\bar{N}$) present on study plots during each trapping period were estimated using a mean Petersen estimate (Seber 1973:138), according to the equation:

$$\overline{N} = \Sigma N_i^* / (s-1)$$

with

$$N_i^* = \frac{(M_i+1)(n_i+1)}{(m_i+1)} - 1$$

and

N_i^* = the estimated population at each stage of the sampling ($i = 2, 3 \ldots s$)

M_i = the number of marked individuals in the population prior to the ith sample

n_i = the number of individuals in the ith sample

m_i = the number of individuals in n_i that were marked previously

s = the number of samples each trapping period.

Besides the several assumptions inherent in mark-recapture analyses (Ricker 1975:81-82), it was assumed that recruitment was negligible. The assumption of an essentially closed population was made on the basis of the relatively short sampling periods. Because of the large proportion of recaptures, $\overline{N}$ was considered a reliable estimator (Seber 1973:61, Ricker 1975:79), and was expected ". . . to have some degree of robustness with regard to departures from the assumptions. . . " (Seber 1973:139). Variance was estimated by: $V[N] = \Sigma(N_i^* - \overline{N})^2/(s-1)(s-2)$, and was considered to be almost unbiased because the N_i^* had the same mean (Seber 1973:138).

Factors that may have affected the trapping results, such as short-term weather conditions or phases of the moon (c.f. Chew and Butterworth 1964, Tanton 1965, O'Farrell 1974, Lockard and Owings 1974) were considered to be inconsequential.

Estimation of Dispersion

The trap-revealed distribution of the four common species inhabiting the study plots was classified as uniform, random or clumped, as determined using Southwood's (1966:36) index of dispersion (χ^2).

Vegetation

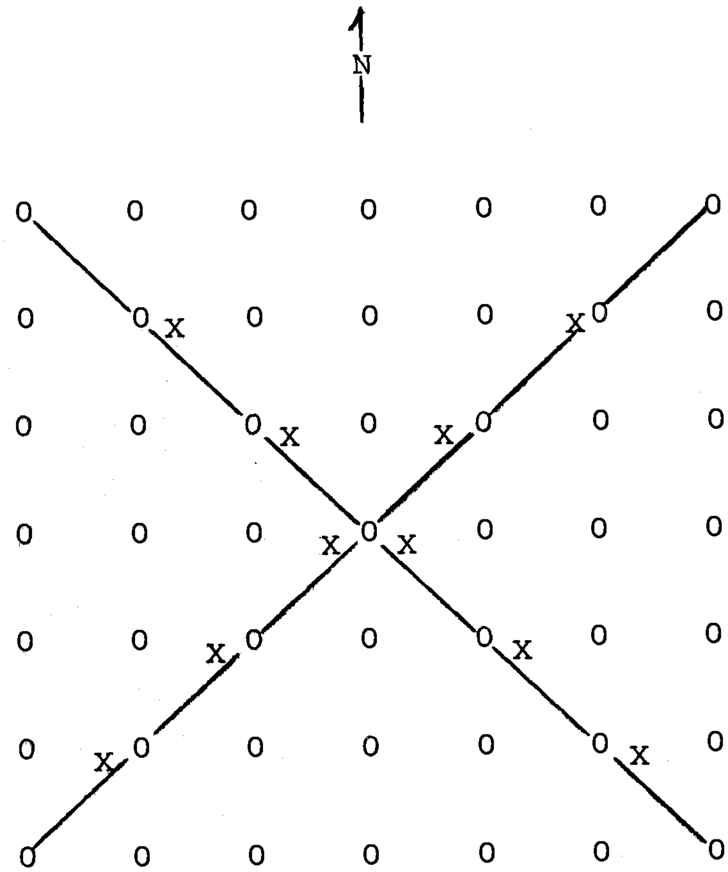
Estimation of Cover

In 1973, vegetation on each study plot was sampled using 1-m^2 quadrats placed at ten random locations within each plot. The frequency of each plant species and an estimate of its density, basal area and percentage cover within each quadrat were recorded. During subsequent field work, cover was estimated on each plot using a Gossen Tri-Lux photoelectric cell. Light intensity was measured at 10 points on the ground and immediately above the vegetation at each point. The percentage difference between readings was considered to represent the amount of cover at each point. All measurements were made between approximately 1100 and1300 each day. Measurements were made along diagonal transects on each plot (Fig. 2) and the average considered an index to the cover present during that trapping period. In addition, in 1975 each plot was visually "divided" into 49 quadrats, each 15.0 m^2 with a trap-site at the center. The percentage of cover in each quadrat was estimated and rated as follows: 0-20 percent = 1; 21-40 percent = 2; 41-60 percent = 3; 61-80 percent = 4; and 81-100 percent = 5 (Myton 1974). For each species of small mammal, a chi-square ratio test was used to determine if the number of captures were equal for each of the five ratings. Expected values were calculated as:

$$E[\text{captures/rating } i] = \frac{\text{total captures on plot}}{\text{trap sites}} \left(\begin{matrix} \text{number of sites} \\ \text{with rating } i \end{matrix} \right)$$

These distributions were considered separately for each plot.

Although an average cover value was calculated for each plot, individual portions of each plot often differed substantially in the amount of cover present. Therefore, the same five-division rating system (Myton 1974) was used to calculate a cover diversity index ("patchiness") from the ten photometric cover readings made on each plot. The formula $1/\Sigma q_i^2$ was used (M'Closkey and Fieldwick 1975), where q_i was the proportion of readings within each of the five cover rankings. Because the minimum value that could be obtained



0 - represents Sherman live-trap site.

X - measurements or samples taken at approximately 20-m intervals.

Figure 2. Diagonal transects on each trapping grid along which samples or measurements were taken for cover, vegetation succulence, soil texture, soil depth, soil strength, soil moisture and number of seeds, on Malheur National Wildlife Refuge from July 1973 through June 1975.

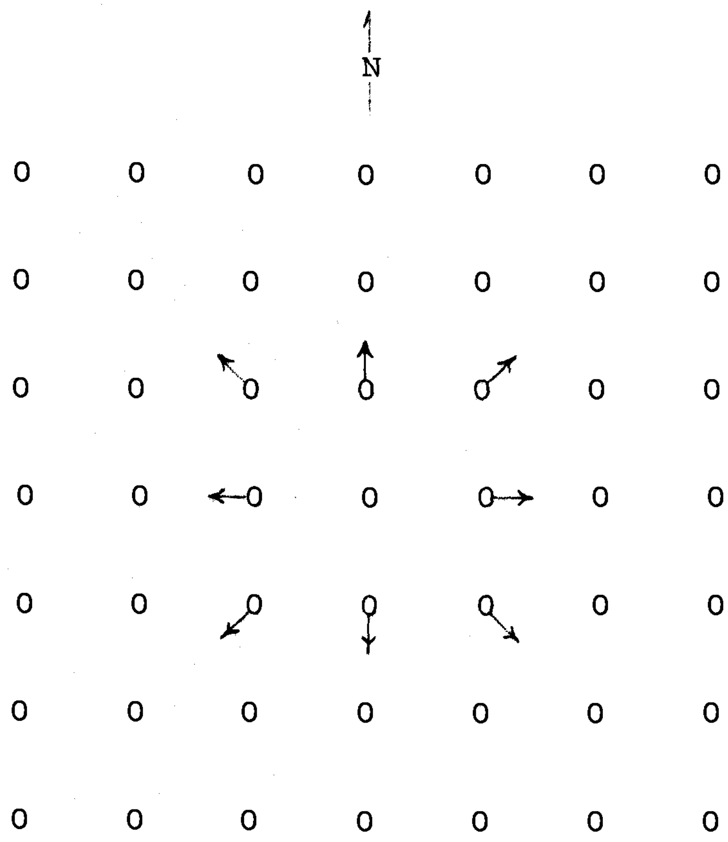
was 1.0, this value was subtracted from each calculation to determine the final index value (Rosenzwieg and Winakur 1969).

Foliage Height Diversity

During the initial trapping period on each plot in 1974, the foliage height diversity (FHD) of the vegetation was measured using general methods described previously (MacArthur and MacArthur 1961, Rosenzwieg and Winakur 1969, M'Closkey and Lajoie 1975). Vegetative density was measured in a different direction from each of eight trap-stations (Fig. 3) at heights of 7.6, 15.0, 30.0, 46.0 and 61.0 cm above the ground. An average of the eight measurements at each height was converted to a proportion of the vegetation (q_i) and the FHD computed using $1/\Sigma q_i^2$, with $i = 1, 3$ and 5 only. Again, 1.0 was subtracted from each calculation. Thus, the vegetation was considered to occupy three distinct layers: below 15.0 cm (P_1); between 15.0 and 46.0 cm (P_2); and above 46.0 cm (P_3). The FHD provided a quantitative measure of the horizontal "layering" of the vegetation, while the patchiness component provided a measure of the "vertical" variation in the vegetation.

Vegetative Moisture

The percentage of vegetative moisture (succulence) was determined each trapping period beginning in 1974. Ten samples were



0 - represents Sherman live-trap site.

Figure 3. Trap location and direction from which measurements of foliage height diversity were made on each study plot on Malheur National Wildlife Refuge during the initial trapping period of 1974.

collected along diagonal transects (Fig. 2) and an average succulence value computed. The procedure involved clipping vegetation from an approximate 1-m^2 area, placing samples in airtight cans and weighing each sample before and after oven drying at about 63°C, to determine the weight of water in the material. The ratio of water weight to dry weight was considered the percent moisture content (Dawson 1972).

Estimation of Seed Abundance

To determine the relative number of seeds present on plots in sagebrush and greasewood areas, and that presumably were available to small mammals, soil samples were collected from plots in these habitats during trapping periods. Plots on marsh and grassland areas were not amenable to the technique and were not considered. About 2.0 cm of topsoil were removed from 1/4-m^2 quadrats, with samples collected at ten sites along diagonal transects of each plot (Fig. 2). About 6.0 liters of soil per plot per trapping period were collected. Samples were placed in paper bags and returned to the laboratory. Each sample was sifted through three Tyler Standard sieves of decreasing mesh size; 1.98 mm, 0.99 mm and 0.49 mm. Material retained at each sieve was examined for seeds with the unaided eye or using a low power binocular microscope. Because no seeds were apparent, all retained material was placed in labeled envelopes. The contents of several of these envelopes were then subjected to combinations of seed-separating processes available at the Hyslop Crop Science Field Laboratory, Oregon State University. Separation processes included "shaker trays", forced air columns of variable intensity, and "vibrator trays" covered with fabric of various textures. Several attempts at seed separation, using material retained at each sieve size, failed to separate seeds from the sample material. Further efforts were discontinued.

Soils

Texture

The soil texture of each study plot was determined once in 1973 and was considered to remain constant for the duration of the field work. Ten soil subsamples were collected from depths of approximately 15.0 cm along diagonal transects (Fig. 2). Subsamples were combined to form a single sample that was analyzed for composition of sand, silt and clay by the Bouyoucos method (Dawson 1972).

Depth and Sheer Stress

The mean soil depth on each plot was estimated by forcing a sharpened steel probe, 1.0 cm in diameter, into the ground to a depth of 102.0 cm. If an obstruction was met prior to this depth, the distance from ground surface to the obstruction was recorded. An average depth was determined from ten probings made along diagonal transects (Fig. 2).

A mean value of the soil sheer stress ("strength") on each plot was measured once during the initial trapping period of 1974, using a Soil Test pocket penetrometer. A spring calibrated from 0 to 4.5 units was compressed while a blunt rod, 6.0 mm in diameter, was gradually pushes into the soil to a depth of 6.0 mm. The index value, measured in kg/cm^2 (tons/ft^2), was in direct proportion to the soil strength. Ten measurements, made along diagonal transects (Fig. 2), were averaged to obtain a mean value.

Diversity values for both soil depth and soil strength were calculated using $1/\Sigma q_i^2$. For soil depth, diversity was computed on the basis of four equal rankings (q_i) of 25.4 cm each. Diversity for soil strength also was computed on the basis of four rankings; 0-1.12, 1.13-2.25, 2.26-3.39 and 3.40-4.50 kg/cm^2.

Soil Moisture

The percentage soil moisture on each plot was estimated each trapping period following the procedure described to estimate vegetative succulence (Dawson 1972). Ten samples were collected from a depth of 15.0 cm along the diagonal transects (Fig. 2) and an average value computed.

Regression Analyses

Linear regression analyses were used to determine the relationship between the estimated mean density of each species of small mammal and concurrently measured, independent habitat parameters. Stepwise, multiple regression analyses also were employed, using the CDC 3300 computer at Oregon State University. Habitat variables and associated densities of small mammal species in each of the four community types were analyzed in three groupings: 1) for the entire study period; 2) for all periods exclusive of 1973, so that the effects of vegetative succulence and patchiness could be evaluated; and 3) for the initial trapping period of 1974, because foliage height diversity and soil strength were measured only during this period.

Besides the relationship between the mean density of small mammals and concurrently measured habitat factors, regressions were calculated to evaluate possible 3-month "lag effects" during the 6-month trapping period of 1974. That is, the habitat variables on each plot during June through August 1974 were correlated with the mean density of each species during September through November 1974.

Correlations were considered to be statistically significant if $\underline{P} < 0.05$.

RESULTS AND DISCUSSION

During the field work, 26,460 trap-nights on the study plots produced 4,717 captures of small mammals. These captures involved 1,580 individuals and represented 4 mammalian orders (Table 1). Three orders were represented by single species and were considered incidental to the study as traps were not set for them. Although 13 species of rodents from 4 families were captured, only 4 species; deer mice, montane voles (*Microtus montanus*), Great Basin pocket mice (*Perognathus parvus*) and least chipmunks (*Eutamias minimus*), which together comprised 90.1 percent of the small mammals captured, were considered in detail in the analyses and discussion.

Predominant Species of Small Mammals

Great Basin Pocket Mouse

Density--Great Basin pocket mice were resident only on plots in sagebrush or greasewood communities. In sagebrush communities, among-plot variation in the density of pocket mice differed seasonally only by a factor of about 4. Within-plot variation did not exceed a factor of 5 seasonally (Table C). In the greasewood areas however, among-plot differences in the density of pocket mice differed by as much as a factor of about 7; there was an equivalent difference in density within plots (Table D). Although densities were generally

Table 1. Total number of individuals of each mammalian species captured on study plots in the four predominant types of terrestrial plant communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

Order	Species	Community type				
		Sagebrush [a]	Greasewood [b]	Marsh [c]	Grassland [d]	Total
Rodentia	Peromyscus maniculatus	153	231 (245) [e]	59 (86)	1 (2)	444
	Microtus montanus	0	7 (7)	330 (478)	100 (171)	437
	Perognathus parvus	206	72 (76)	5 (7)	0	283
	Eutamias minimus	101	159 (169)	0	0	260
	Reithrodontomys megalotis	1	13 (14)	36 (52)	21 (36)	71
	Dipodomys ordii	30	11 (12)	0	0	41
	Dipodomys microps	9	2 (2)	0	0	11
	Onychomys leucogaster	7	0	0	0	7
	Microtus longicaudus	0	0	3 (4)	0	3
	Microdipodops megacephalus	3	0	0	0	3
	Spermophilus townsendii	2	1 (1)	0	0	3
	Neotoma lepida	2	0	0	0	2
	Thomomys talpoides	1	0	0	0	1
Carnivora	Mustela frenata	0	1 (1)	2 (3)	0	3
Insectivora	Sorex vagrans	0	0	10 (14)	0	10
Lagomorpha	Sylvilagus nuttallii	1	0	0	0	1
	Totals	515	498 (528)	445 (645)	122 (209)	1,580

[a] Involved 5 plots and 8,232 trap nights.

[b] Involved 5 plots and 7,742 trap nights.

[c] Involved 4 plots and 5,684 trap nights.

[d] Involved 4 plots and 4,802 trap nights.

[e] Because unequal effort was expended in each habitat type, numbers in parenthesis represent relative totals for animals captured in greasewood, marsh and grassland habitats, based on a total effort comparable to that made in sagebrush areas.

lower on the greasewood than the sagebrush plots, in both habitat types peak numbers of pocket mice generally were trapped from late April to early June. The lowest population densities occurred from late June through mid-August. These fluctuations in population density were similar in both timing and magnitude to those of a population of P. parvus studied by O'Farrell et al. (1975) in shrub-steppe habitat in southeast Washington.

An apparent increase in the density of pocket mice on most plots occurred in the fall. This was probably the result of increased numbers of animals that became susceptible to trapping when temperatures became cooler and surface activity increased.

Reproduction--Male pocket mice on sagebrush and greasewood plots were in breeding condition from early May until early August. Peak breeding activity probably occurred in early June, a period not adequately represented by trapping data. Males were reproductively active about a month before the females, based on the percentage in reproductive condition and the biased sex ratios on both habitat types during May (Table 2). Pregnant females were trapped almost exclusively in June and no reproductively active pocket mice were trapped after 29 August in either habitat type.

Juvenile pocket mice were trapped from late April to early September on plots in sagebrush areas, although the majority was found from June through August. Juveniles were trapped only during

Table 2. Monthly mean percentage of juveniles, percentage of adults in breeding condition and adult sex ratios for populations of Great Basin pocket mice occupying plots in the two types of shrub communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

	May		June		July		August		September		October		November	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Sagebrush														
Juveniles	3	5	3	27	11	28	9	24	2	5	0	0	0	0
Adults Repro. Active														
♂	38	24	6	100	17	6	17	6	25	0	5	0	5	0
♀	21	0	2	100	11	18	12	25	15	0	2	0	2	0
Sex Ratio (♂:♀)	38:21[a]		6:2		17:11		17:12		25:15		5:2		5:2	
Greasewood														
Juveniles	0	0	1	12	3	38	5	26	0	0	0	0	0	0
Adults Repro. Active														
♂	26	73	5	80	5	100	10	40	3	0	1	0	0	0
♀	4	50	2	100	0	0	4	25	1	0	0	0	1	0
Sex Ratio (♂:♀)	26:4[a]		5:2		5:0[a]		10:4		3:1		1:0		0:1	

[a]Significant difference (X^2 test, $\underline{P} < 0.05$).

the latter 3 months in greasewood areas. This may have resulted because the sagebrush communities, with a greater composition of sand in the soil, generally desiccated faster in the spring than greasewood plots (Tables E and F). In this respect, sagebrush areas may have represented the preferred habitat of this species. In both habitat types though, the largest proportion of the population of pocket mice contributed by juveniles occurred during July (Table 2).

Dispersion--The trap-revealed dispersion of pocket mice on all ten plots in sagebrush or greasewood communities differed significantly from random, and on all plots a clumped distribution pattern was evident.

On the 3 plots where 60 or more capture records of pocket mice were obtained, a significant relationship was evident between their trap-revealed distribution and the density of cover. Significantly fewer pocket mice than expected were trapped in quadrats with less than 40 percent cover, while more pocket mice than expected were trapped in quadrats with greater than 40 percent cover (Table 3).

The preference of pocket mice for areas of relatively dense cover undoubtedly was a response to the combined effects of several factors. Increased vegetation, in conjunction with the body shape and mode of locomotion of the species, possibly reduced the rate of predation (Rosenzwieg and Winakur 1969, Brown and Lieberman 1973, Kritzman 1974), increased forage availability and decreased competition from other heteromyids (O'Farrell 1975); and possibly in a secondary manner, beneficially affected microhabitat evaporation rates, humidity and air temperature (Beatley 1976).

Table 3. Cover ratings (Myton 1974) and associated number of captures of Great Basin pocket mice on plots in shrub communities on Malheur National Wildlife Refuge during spring, 1975. Plots on which 20 or more specimens were captured.

Plot	Rating	No. sites with rating	Observed captures	Expected captures
Sagebrush #2[a]	1	0	--	--
	2	4	2	7.8
	3	45	93	87.3
	4	0	--	--
Sagebrush #5[b]	1	22	31	48.2
	2	14	35	30.7
	3	10	30	21.9
	4	3	11	6.6
Greasewood #5[c]	1	30	32	44.1
	2	18	37	26.5
	3	1	3	1.5
	4	0	0	--

[a]Significant difference $\chi^2 = 4.65$, $\underline{P} < 0.05$.
[b]Significant difference $\chi^2 = 12.72$, $\underline{P} < 0.01$.
[c]Significant difference $\chi^2 = 9.11$, $\underline{P} < 0.025$.

Correlations--Although vegetation was of obvious importance in the local distribution of pocket mice, in all sagebrush or greasewood areas the abundance of this species was significantly correlated concurrently only with edaphic factors. A direct correlation between the population density of pocket mice and the percentage of sand on each plot was evident (Fig. 4A). For the multiple regression analysis, the inverse correlations of density with soil depth diversity on the sagebrush plots ($r^2 = 0.51$, $P < 0.02$), and with the percentage of clay on the greasewood plots ($r^2 = 0.48$, $P < 0.02$) suggested that these factors were of significance in the density of pocket mice during the summer and possibly throughout the year. The ability of pocket mice to dig through the surface layer of the soil was of obvious importance in their fossorial activities. The general importance of a suitable edaphic component of the environment was further suggested by the other correlates to population density; inverse relationships with the percentage of clay in the soil (Fig. 4B), and a direct correlation with soil depth ($r^2 = 0.17$, $P < 0.05$) in sagebrush areas. These edaphic factors were probably relevant directly, and through interrelationships with other aspects of the soil that affected burrow construction and stability. For example, soil texture had a direct influence on several aspects of soil moisture, including depth and rate of percolation, retention and evaporation rates (Krynine 1947:33, 56, Beatley 1976). Considering cross-correlations in greasewood areas, the mean soil moisture was inversely correlated with percentage of sand ($r^2 = 0.92$, $P < 0.005$), as was percentage cover ($r^2 = 0.44$, $P < 0.02$). In turn, these factors may have influenced soil strength (Hardy 1945). Soil depth was an important determinant of potential burrow depth (Rickard 1960, Kritzman 1974) and the gradient of soil

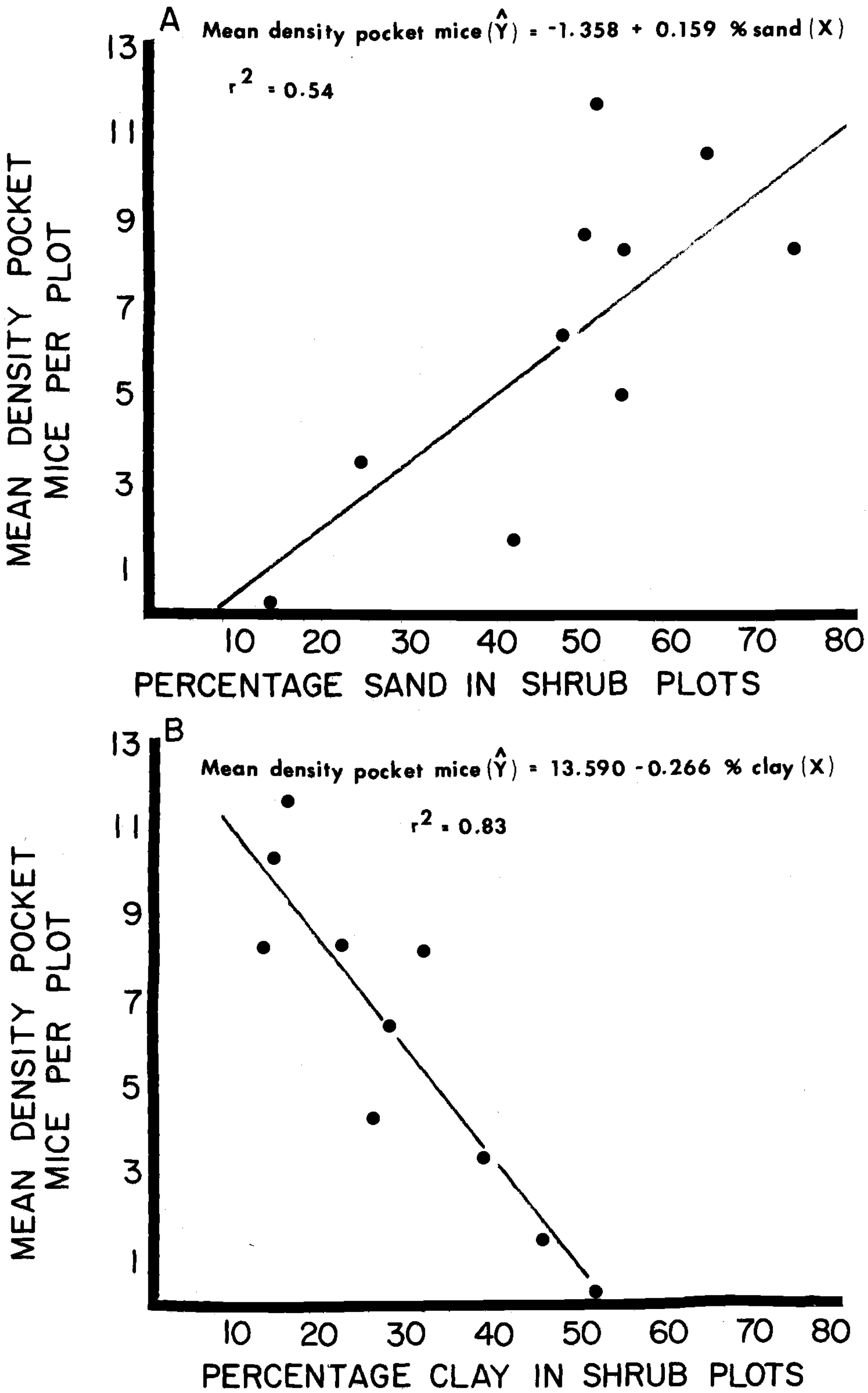


Figure 4. Relationship between components of soil texture and mean density of Great Basin pocket mice on 10 study plots in shrub communities on Malheur National Wildlife Refuge from July 1973 through June 1975. a) Percentage of sand, B) Percentage of clay.

temperatures throughout the year (Kenagy 1973, O'Farrell et al. 1975). As expected, however, the correlations evident in this study do not apply to all species of pocket mice. Rosenzwieg and Winakur (1969) reported only slight correlation with soil strength and none with texture or depth relative to the distribution and abundance of five other species of pocket mice in Arizona.

The only vegetative factor that was correlated with the density of pocket mice was apparent when a lag-effect was considered, and then only on plots in sagebrush areas. A direct relationship existed between the vegetative succulence from June to mid-August and the density of pocket mice from mid-August through November ($r^2 = 0.96$, $\underline{P} < 0.01$).

The relationship between the availability of green vegetation and reproductive success of desert rodents has been suggested (Bradley and Mauer 1973, Van De Graaff and Balda 1973, French et al. 1974). A corresponding lag between the quality and quantity of seeds produced and available to rodents, and the degree of moisture available to the plants, might be expected (Brown 1973, Kritzman 1974, O'Farrell et al. 1975). Vegetative succulence (Table G) was at a maximum 2 to 3 months prior to the peak occurrence of juvenile pocket mice on the sagebrush plots. Thus, the availability of high quality seeds may have been a factor in adult reproductive activity and survival of offspring on the sagebrush areas. Chew and Butterworth (1964) observed 1-year lag periods in the population density of Merriam's kangaroo rat (*Dipodomys merriami*) relative to changes in the availability of green vegetation. Reichman and Van De Graaff (1975), working with the same species, reported a significant relationship between reproduction and green vegetation without a lag period, but even higher correlation coefficients when 2- to 3-month lag periods were introduced. The absence of a significant relationship between pocket mice and vegetative succulence on greasewood plots may have been caused by this shrub being representative of generally more mesic habitats.

Least Chipmunk

Density--Least chipmunks occurred only in sagebrush or greasewood communities. In the sagebrush community type, during only two trapping periods did the density of chipmunks among plots differ by a factor of as much as 3. Within-plot fluctuations in population density, with the exception of plot no. 1, varied by an equivalent amount (Table C). In greasewood, among plot variation in population densities varied seasonally by a factor of about 6, with the exception of the 1973 trapping period. There was an equivalent variation within-plots seasonally (Table D). The mean density of chipmunks was greater in greasewood than in sagebrush areas. In neither community type however, was there a season during which peak numbers were evident. Vaughan (1974) also noted a fairly stable population density for this species in northern Colorado.

Reproduction--Male chipmunks may have been reproductively active in both community types about 1 month before the females, as suggested by the percentage of each sex in breeding condition and the biased sex ratio during May (Table 4). Breeding apparently was confined to a fairly brief period, with peak activity in May, or possibly before when trapping was not conducted. The number of chipmunks in breeding condition declined rapidly in both community types throughout the summer. No reproductively active chipmunks were trapped after 31 July in the greasewood areas or after 29 August in sagebrush areas. Davis (1939) and Gordon (1943) reported that this species mated from early to mid-spring in the northern part of its range, while Negus and Findley (1959) reported no sexually active least chipmunks occurring after late June in northwest Wyoming.

Of the 260 chipmunks captured throughout the study, only 1 was considered to be a juvenile. Because of the timing of breeding, juveniles were probably most numerous in early June, a period during which trapping was not conducted. This was further suggested by the results of Hall (1946) and Linsdale (1938), who reported parturition in least chipmunks in Nevada occurred during May and early June. Tevis (1958) found gravid least chipmunks during mid-April in northeastern California. Also, the criterion of age may have been inadequate to distinguish juvenile chipmunks.

Table 4. Monthly mean percentage of juveniles, percentage of adults in breeding condition and adult sex ratios for populations of least chipmunks occupying plots in the two types of shrub communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

	May		June		July		August		September		October		November	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Sagebrush														
Juveniles	0	0	1	10	0	0	0	0	0	0	0	0	0	0
Adult Repro. Active														
♂	19	95	7	29	23	4	9	22	18	0	0	0	0	0
♀	5	40	2	50	18	13	3	0	6	0	0	0	0	0
Sex Ratio (♂:♀)	19:5[a]		7:2		23:8[a]		9:3		18:6		-		-	
Greasewood														
Juveniles	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adult Repro. Active														
♂	16	88	4	75	26	23	30	0	24	0	5	0	0	0
♀	5	40	1	0	21	19	2	0	14	0	11	0	0	0
Sex Ratio (♂:♀)	16:5[a]		4:1		26:21		30:2[a]		24:14		5:11		-	

[a]Significant difference (X^2 test, $\underline{P} < 0.05$).

Dispersion--On all plots where more than 23 capture records of chipmunks were obtained, their dispersion was clumped. On none of the plots was there a relationship between dispersion and the amount of vegetative cover. On only 1 plot were there as many as 60 location records, however.

Correlations--On both shrub areas, a positive correlation was evident between the density of chipmunks and the mean depth of soil (Fig. 5), and with soil strength (Fig. 6). On sagebrush areas a positive correlation was found between density and diversity of soil strength ($r^2 = 0.88$, $\underline{P} < 0.01$). A direct correlation also was evident between the density of chipmunks and P_2, the proportion of vegetation between 15.0 and 46.0 cm ($r^2 = 0.66$, $\underline{P} < 0.05$). Correlations between the density of chipmunks and habitat factors on the greasewood areas included a direct relationship with the percentage of clay in the soil ($r^2 = 0.72$, $\underline{P} < 0.05$). For the multiple regression analysis, direct correlations were found between the density of chipmunks and soil depth on sagebrush plots ($r^2 = 0.80$, $\underline{P} < 0.02$), and on greasewood plots ($r^2 = 0.47$, $\underline{P} < 0.02$).

Soil strength, diversity of strength and P_2 again were correlated with the density of chipmunks on the sagebrush areas when a 3-month lag period was considered. All these relationships had fairly high correlation coefficients ($r^2 \geq 0.81$, $\underline{P} < 0.025$). An inverse correlation also was evident between the density of chipmunks and

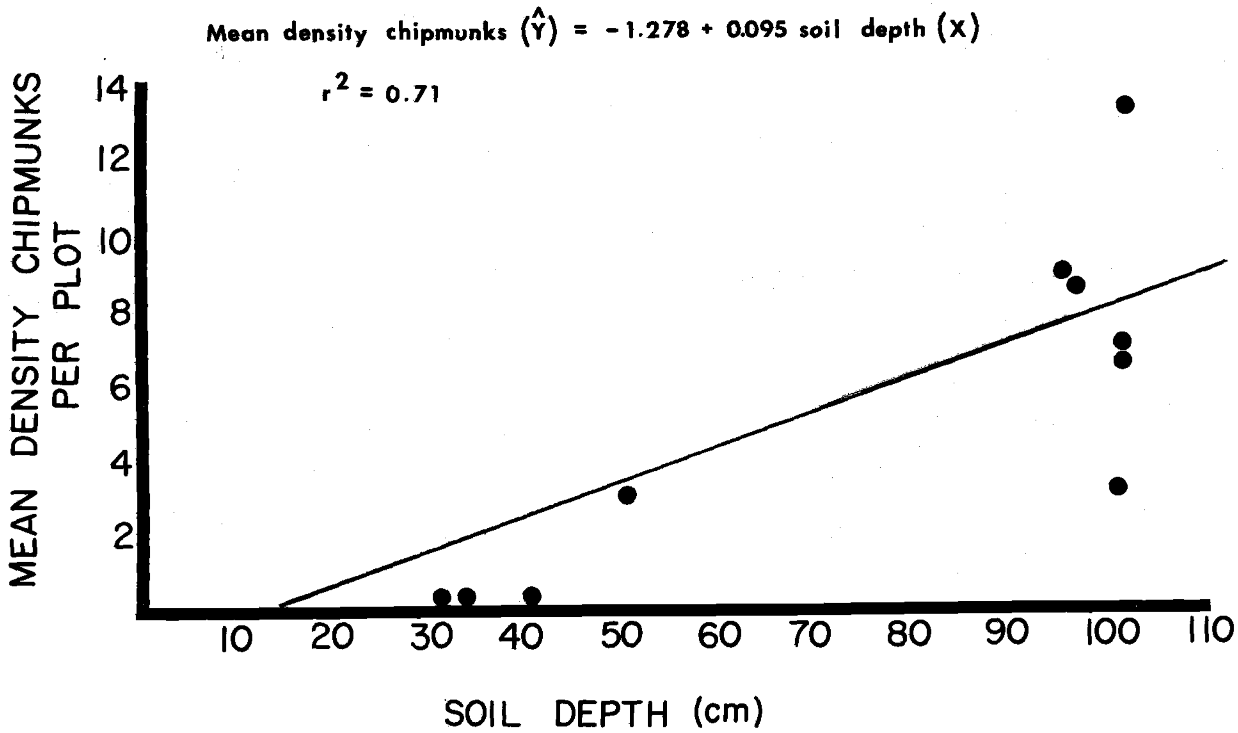


Figure 5. Relationship between the density of chipmunks and soil depth on study plots in two shrub habitat types on Malheur National Wildlife Refuge from July 1973 through June 1975.

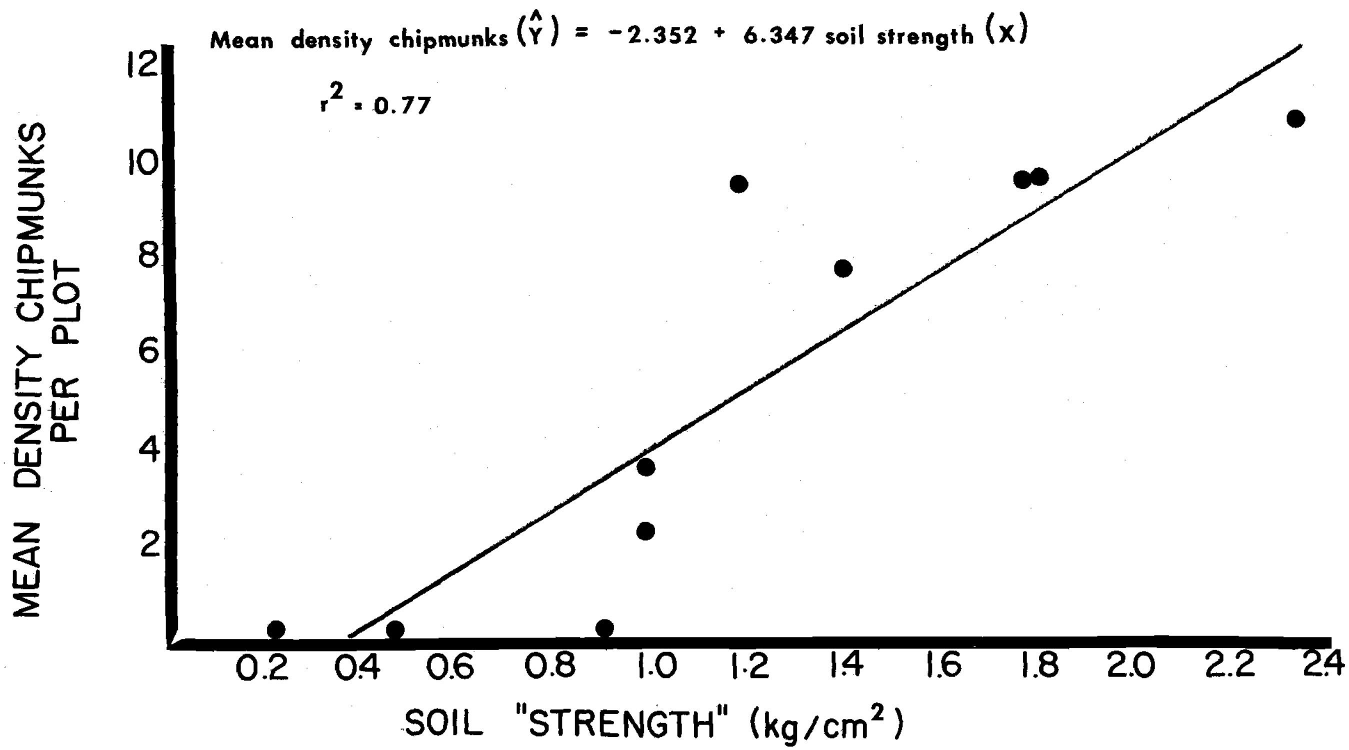


Figure 6. Relationship between the density of chipmunks and soil "strength" on study plots in two shrub habitat types on Malheur National Wildlife Refuge from July 1973 through June 1975.

P_1, the proportion of vegetation below 15.0 cm, when a lag effect was considered ($r^2 = 0.69$, $\underline{P} < 0.05$).

Chipmunks apparently selected both for the presence of vegetation in the P_2 layer and its absence in P_1. This may have been related to two aspects of their behavior. The swift, zig-zag running pattern of this species would probably be aided by relatively sparse vegetation in its immediate path (P_1), which would enhance maneuverability. In conjunction, a canopy of vegetation above this level would not impair movement but could provide a measure of concealment from predators. Because the importance of the vegetation would have involved relative proportions rather than absolute amounts, this might account for the lack of a relationship between the trap-revealed distribution and cover. The structure of the vegetation also may have been a factor in foraging by chipmunks, especially when their scansorial activities were considered (Linsdale 1938, Bailey 1936, Vaughan 1974).

Concurrent edaphic factors were probably of greater significance to this species than vegetation, otherwise the correlations between chipmunk abundance and P_i should have involved less of a lag effect and more of a concurrent relationship. This also was suggested by the lack of relationship between the density of chipmunks and P_i on the plots in greasewood areas. In fact, no vegetative factors were concurrently related with the density of this species in greasewood areas.

The importance of edaphic factors was suggested, however, as they were correlated with the density of chipmunks on both sagebrush and greasewood areas.

As with pocket mice, the soil depth, texture and strength would directly affect chipmunks in the construction and stability of burrows, and indirectly affect aspects of temperature and humidity. The densities of pocket mice and chipmunks were oppositely related to the percentage of clay in the soil; this suggested that chipmunks did not find it as difficult as the smaller pocket mice to dig through a sometimes hard, consolidated soil surface of high clay fraction (Krynine 1947).

The only correlation between the density of chipmunks on the greasewood areas and a factor of the vegetation involved a 3-month lag effect with succulence ($r^2 = 0.81$, $\underline{P} < 0.025$), measured from June to mid-August. Although chipmunks bred primarily before this period, vegetative succulence may have been related indirectly to aspects of forage production and availability. The direct importance of the leaves themselves, as a source of food and water, also may have been a factor in the abundance of chipmunks, and other species of rodents (MacMillen 1964, Kenagy 1973, Kritzman 1974, Beatley 1976).

Deer Mouse

Density--More deer mice were captured than any other species of small mammal. They exhibited the widest local distribution, being considered a resident in sagebrush, greasewood and marsh community types (Table 1). Deer mice were generally most abundant on the greasewood areas, where among-plot variation differed by a factor greater than 3 only in 1973 (Table D). Within-plot fluctuation in the density of deer mice also approached this magnitude. The general densities of deer mice on sagebrush and marsh plots were about equal, with fluctuations in the marsh areas relatively minor (Table H). Populations of deer mice in sagebrush areas exhibited fluctuations in density comparable to those on greasewood areas. Both within- and among-plot variation generally differed by a factor of about 3 (Table C). There was no season during which the density of this species was consistently highest, although density was generally lowest during the summer.

Reproduction--Deer mice were reproductively active during all months that trapping was conducted (Table 5), although a decline in breeding activity was evident during the summer. Parturition occurred at least as early as April in the shrub habitats, as juvenile animals were trapped in May. Peak numbers of juveniles were on the plots in May and in the fall. It was not determined if breeding

Table 5. Monthly mean percentage of juveniles, percentage of adults in breeding condition and adult sex ratios for populations of deer mice occupying plots in sagebrush, greasewood, and marsh community types on Malheur National Wildlife Refuge from July 1973 through June 1975.

	May		June		July		August		September		October		November	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Sagebrush														
Juveniles	7	18	0	0	1	6	5	21	5	29	4	25	4	11
Adult Repro. Active														
♂	18	78	2	50	10	40	15	80	11	45	0	11	20	30
♀	15	72	1	100	7	43	4	25	1	100	3	0	11	18
Sex Ratio (♂:♀)	18:15		2:1		10:7		15:4[a]		11:1[a]		9:3		30:18	
Greasewood														
Juveniles	10	14	3	30	4	11	5	15	10	17	3	20	0	0
Adult Repro. Active														
♂	32	59	3	33	21	76	18	61	30	70	9	22	4	50
♀	28	54	4	75	13	62	10	50	18	72	3	66	3	33
Sex Ratio (♂:♀)	32:28		3:4		21:13		18:10		30:18		9:3		4:3	
Marsh														
Juveniles	0	0	1	11	1	8	0	0	0	0	3	30	1	9
Adult Repro. Active														
♂	2	100	6	100	7	71	8	88	0	0	3	67	7	0
♀	1	0	2	100	4	25	6	83	0	0	4	25	3	0
Sex Ratio (♂:♀)	2:1		6:2		7:4		8:6		-		3:4		7:3	

[a]Significant difference (X^2 test, $P < 0.05$).

continued throughout the year, but considering the usually harsh winter conditions in the Harney Basin, it was doubtful. However, deer mice in sagebrush areas of east-central Washington have bred throughout the year (Scheffer 1924). Length of the breeding season probably varies yearly as a function of weather factors or resource availability (Asdell 1964:265, Sadlier 1974).

Dispersion--The trap-revealed dispersion of deer mice in all habitat types differed significantly from random, and on 10 of 11 plots a clumped pattern was evident. This pattern could not be evaluated in relation to the amount of cover in quadrats in the marsh plots because of too few captures in 1975. The results of this analysis on sagebrush and greasewood plots was inconclusive. On greasewood plot no. 4 and sagebrush plot no. 5, significantly fewer deer mice than expected were captured in portions of those plots with less than 40 percent cover, while greater numbers than expected occurred in portions with more than 40 percent cover. However, on sagebrush plot no. 2 the opposite relationship was apparent (Table 6), and on the remaining five plots where sufficient capture records were available to allow analysis, there were no significant relationships between the amount of cover and the dispersion of deer mice ($\underline{P} > 0.05$).

These results reflect the range of relationships relative to cover previously reported for this species. A direct relationship between amount of cover and the local distribution and abundance of

Table 6. Cover ratings (Myton 1974) and associated number of captures of deer mice on plots in shrub communities on Malheur National Wildlife Refuge during spring, 1975. Plots on which 20 or more specimens were captured.

Plot	Rating	No. sites with rating	Observed captures	Expected captures
Sagebrush #2[a]	1	0	0	--
	2	4	5	1.6
	3	45	15	18.4
	4	0	0	--
Sagebrush #5[b]	1	22	14	26.0
	2	14	19	16.5
	3	10	21	11.8
	4	3	4	3.5
Greasewood #4[c]	1	12	16	22.6
	2	27	35	50.8
	3	4	11	7.5
	4	4	16	7.5
	5	2	14	3.8

[a]Significant difference $\chi^2 = 7.53$, $\underline{P} < 0.01$.

[b]Significant difference $\chi^2 = 13.11$, $\underline{P} < 0.005$.

[c]Significant difference $\chi^2 = 45.48$, $\underline{P} < 0.005$.

Peromyscus was described by Allred and Beck (1963). However, the proportion of cover did not exceed 25.0 percent on any of the areas sampled by these authors. An inverse relationship between these parameters was reported for several habitat types, including grassland and cultivated areas (Phillips 1936, LoBue and Darnell 1959, Tester and Marshall 1961), desert shrub (MacMillen 1964), and sites disturbed by strip-mining (Dusek and McCann 1975). In similar habitats, other researchers found no relationship between amount of cover and local distribution or abundance of deer mice (Rickard 1960, Verts 1957). Because these studies involved a variety of vegetative communities, and the results of the present study were equivocal, no general relationship between the local distribution or abundance of deer mice and amount of cover can be made.

Correlations--A significant correlation was evident between the density of deer mice and the mean amount of cover only during the summer of 1974 on plots in greasewood habitat ($r^2 = 0.75$, $\underline{P} < 0.05$). The only other relationship between the density of deer mice and a vegetative factor, that did not involve a lag effect, concerned the physical structure of the foliage. There was a direct correlation between the density of deer mice and the amount of vegetation at the three heights used to measure foliage height diversity ($\Sigma q_{1,3,5}$). This correlation was evident on plots in both sagebrush areas ($r^2 = 0.98$, $\underline{P} < 0.001$) and greasewood areas ($r^2 = 0.86$,

$\underline{P} < 0.025$). As expected, only on greasewood areas was a direct relationship evident between $\Sigma q_{1,3,5}$ and cover ($r^2 = 0.83$, $\underline{P} < 0.025$). No relationship was evident between $\Sigma q_{1,3,5}$ and cover in the sagebrush areas.

It appeared that deer mice in shrub communities selected for increased foliage, but only at certain interspersed levels of the vegetative profile, at least in sagebrush areas (Fig. 7), rather than a continuum of foliage above or below a particular height. Whether this relationship was of direct adaptive significance relative to aspects of predator avoidance, foraging or general scansorial tendencies (Horner 1954), or was indirectly associated with some other factor, was not readily apparent.

Although they may utilize burrows, the fossorial abilities of deer mice are not particularly well developed (Bailey 1936, King 1968). It was not surprising therefore, that edaphic factors were of less importance in the local distribution and abundance of deer mice than for pocket mice or chipmunks. In marsh areas, a slight positive correlation existed between the density of deer mice and the percentage of sand in the soil ($r^2 = 0.37$, $\underline{P} < 0.05$). This relationship was also noted in the multiple regression analysis ($r^2 = 0.32$, $\underline{P} < 0.05$). On greasewood areas, an inverse relationship was evident between these two factors ($r^2 = 0.80$, $\underline{P} < 0.025$), as well as a direct correlation between the density of deer mice and the percentage of soil

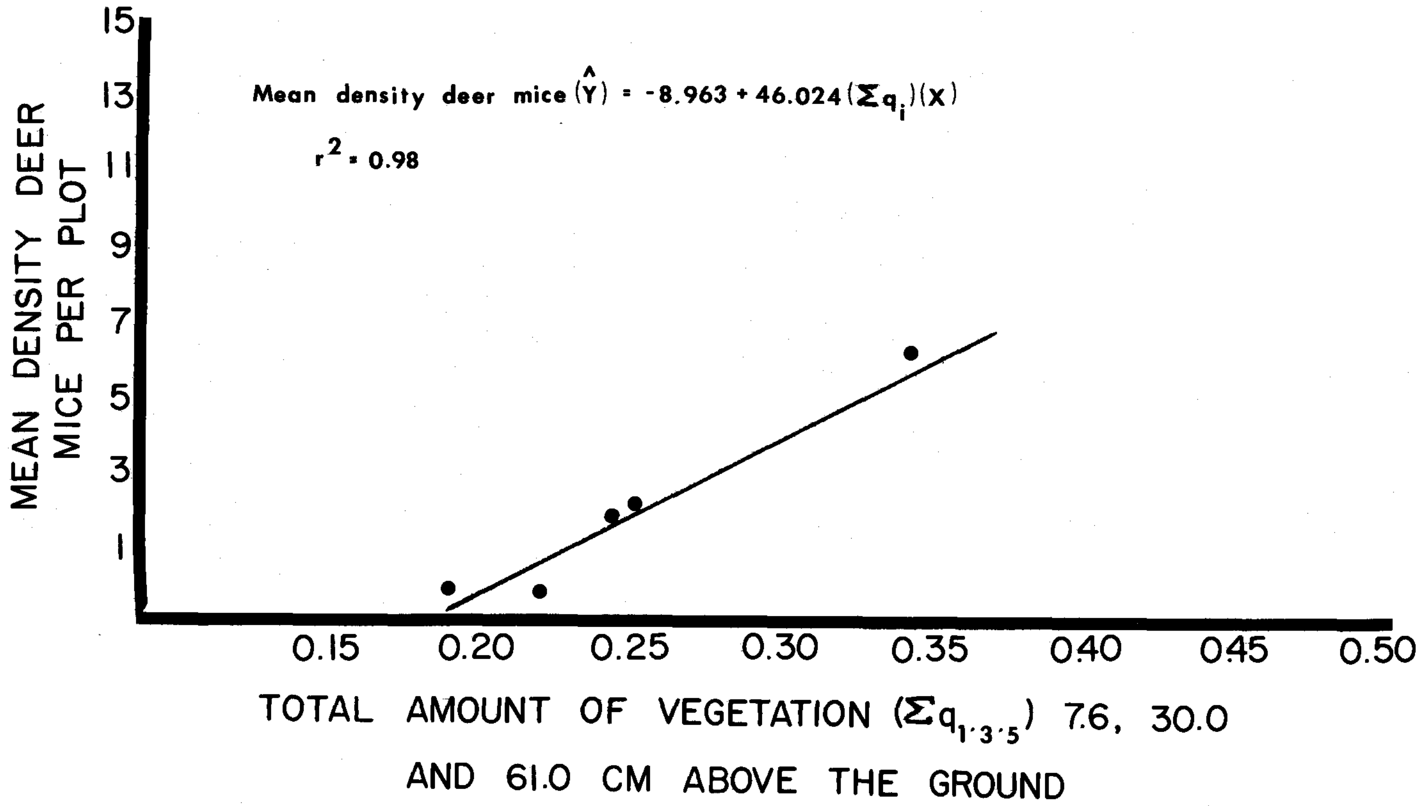


Figure 7. Relationship between the mean density of deer mice and the total amount of vegetation at the three heights used to measure foliage height diversity on five study plots in sagebrush habitat on Malheur National Wildlife Refuge during the initial trapping period of 1974.

moisture ($r^2 = 0.30$, $\underline{P} < 0.01$). The density of deer mice was also correlated with soil moisture in the multiple regression analysis ($r^2 = 0.35$, $\underline{P} < 0.05$). Therefore, deer mice exhibited an opposite response to the percentage of sand on marsh and greasewood areas, habitats generally subjected to large differences in the amount of free water associated with them (Table F).

The permeability and drainage capabilities of soils vary directly with their percentage of sand (Krynine 1947). The opposite response of deer mice to the percentage of sand on marsh and greasewood plots may have resulted from an effort by deer mice to select an "optimal" moisture range within the continuum of soil moisture conditions that could be tolerated. That is, "wetter" arid areas and "drier" wet areas. During the summer at least, the physiological and metabolic response of deer mice to heat stress might have been a factor in the apparent preference of this species for greasewood habitat, the more mesic of the arid habitats. Deer mice have poorly developed thermoregulatory abilities above thermoneutrality, and they subsequently depend on the availability of environmental water to maintain thermal balance (Murie 1961).

The only other correlations between the density of deer mice and habitat factors involved a 3-month lag effect with the soil moisture ($r^2 = 0.96$, $\underline{P} < 0.005$), and the vegetative succulence ($r^2 = 0.68$, $\underline{P} < 0.05$), on plots in the greasewood habitat. Green vegetation was probably an important factor in the reproductive efforts of deer mice, as with other cricetids (Negus and Pinter 1966). It was noted that a 3-month lag effect relationship between vegetative succulence and small mammal abundance was statistically significant for all three species common in the shrub communities, but only in the one habitat type where each species attained its greatest abundance.

Montane Vole

Density--In marsh areas, montane voles were resident only on plots no. 3 and 4. During the four-day trapping periods of 1973, 65 individuals were captured on plot no. 3, and 71 on plot no. 4. Although the short trapping periods resulted in high standard deviations (Table I), the density of voles during this period was the highest of any small mammal during the study. Densities declined sharply after the initial trapping period. In 1975, the population density of voles on marsh plot no. 3 was reduced from the 1973 estimate by a factor of at least 20. Although the population densities of voles in grassland areas were generally lower than in marsh areas, the grassland plots were continuously altered by land-use practices throughout the field work and trends in the density of voles were difficult to determine. However, among- and within-plot fluctuations apparently varied by a factor of about 2 during the initial 3 trapping periods.

Reproduction--The reproductive data concerning voles were not as complete as for the other species of small mammals. Reproductively active voles were trapped in marsh areas only from July through September (Table 7). However, montane voles were undoubtedly breeding during the spring months (Bailey 1936:203), when trapping was not conducted in marsh or grassland communities. Also, considering the short gestation period of this species (Asdell 1964), and juvenile voles were trapped in early November, breeding must also have occurred in October. There was no period during which the juvenile increment of the population or the percentage of adults in breeding condition was consistently largest.

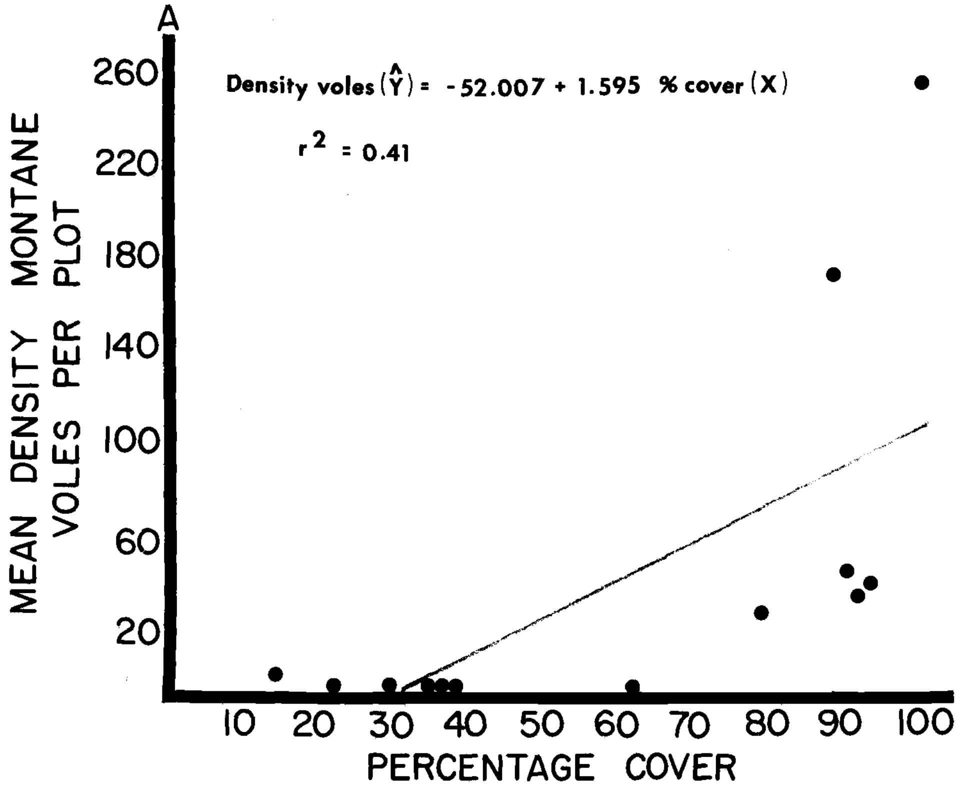
Dispersion--The trap-revealed dispersion of voles on all plots differed significantly from random, and a clumped pattern was evident. On the only plot where the analysis could be made, the dispersion of voles was related to the amount of cover. Voles were trapped significantly more often in quadrats where cover was greater than 80 percent (Table 8).

Correlations--There was a direct correlation between the estimated population density of voles and the mean amount of cover on plots in marsh and grassland communities (Fig. 8). In a related manner, an inverse relationship was evident between the density of voles and the patchiness of cover in these habitat types (Fig. 9). For the multiple regression analysis, the patchiness of cover was again of

Table 7. Monthly mean percentage of juveniles, percentage of adults in breeding condition and adult sex ratios for populations of montane voles occupying plots in the marsh and grassland communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

	May		June		July		August		September		October		November	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Marsh														
Juveniles	0	0	-		11	15	13	13	16	28	22	42	13	29
Adults Repro. Active														
♂	5	0	-		43	14	50	6	24	8	19	0	21	0
♀	2	0	-		18	11	32	16	27	18	11	0	11	0
Sex Ratio (♂:♀)	5:2		-		43:18[a]		50:32[a]		24:27		19:11		21:11	
Grassland														
Juveniles	-		-		-		13	22	1	50	-		10	26
Adults Repro. Active														
♂	-		-		-		25	24	1	0	-		17	0
♀	-		-		-		22	25	0	0	-		11	0
Sex Ratio (♂:♀)	-		-		-		25:22		1:0		-		17:11	

[a]Significant difference (X^2 test, $P \leq 0.05$).



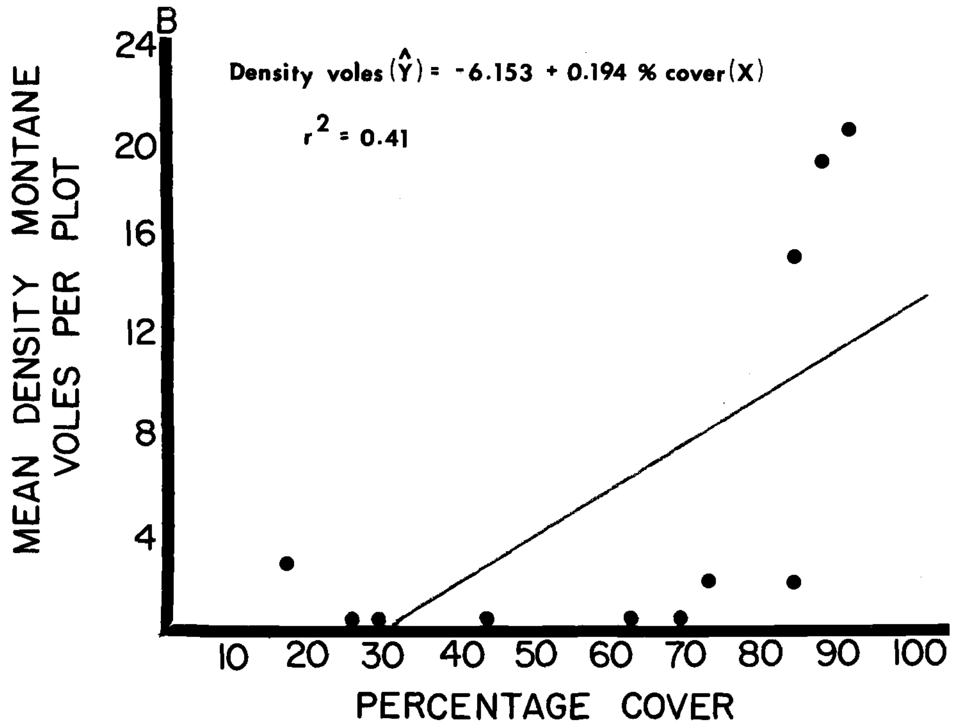


Figure 8. Relationship between the mean density of montane voles and the amount of cover on study plots on Malheur National Wildlife Refuge from July 1973 through June 1975. A) Marsh plots, B) Grassland plots.

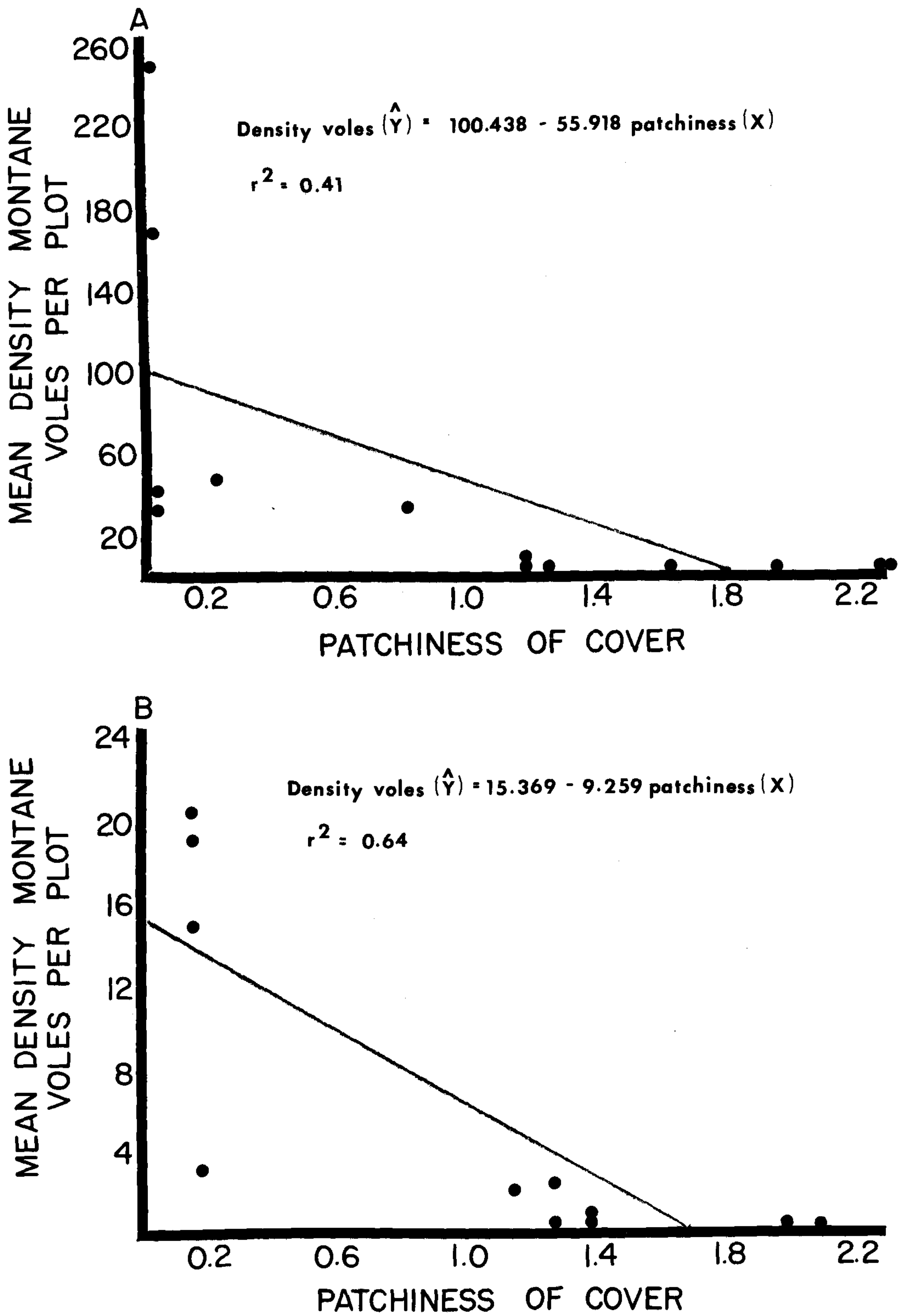


Figure 9. Relationship between the mean density of montane voles and the patchiness of the vegetative cover on marsh and grassland plots on Malheur National Wildlife Refuge from July 1973 through June 1975. A) Marsh plots, B) Grassland plots.

significance on marsh areas ($r^2 = 0.41$, $\underline{P} < 0.05$). The direct relationship between the occurrence of M. montanus and dense cover is well documented (Bailey 1936, Hodgson 1972), as it is for several other species of microtines (Eadie 1953, Mossman 1955, Pearson 1959, Miller and Getz 1972). As discussed by Getz (1961), it would be difficult to separate the relative functions of cover and importance to montane voles in terms of protection from predation, microhabitat modification and food resources. The importance of cover to this species was further demonstrated by a comparison of its densities on grassland plots no. 3 and 4. These plots were sampled concurrently in August and again in November 1974. During the initial trapping period, there was no statistical difference in the estimated density of vole populations on each plot. Plot no. 3 was undisturbed prior to the second trapping period and the density of voles was unchanged from the August estimate. However, plot no. 4 was mowed prior to the second trapping period, which greatly reduced cover (Table J); only one individual was caught in November (Table K). A similar situation was reported by LoBue and Darnell (1959) for a harvested alfalfa field.

No other vegetative or edaphic factor was concurrently related with the density of montane voles. When a 3-month lag effect was considered on the marsh plots, correlations were again evident between the density of voles and amount of cover ($r^2 = 0.98$, $\underline{P} < 0.025$). No lag effects were apparent in the plots on grassland areas, probably because the populations were disrupted when three of the four plots were mowed between the two trapping periods of 1974.

Table 8. Cover ratings (Myton 1974) and associated number of captures of montane voles on plots in marsh or grassland communities on Malheur National Wildlife Refuge during spring, 1975. Plots on which 15 or more specimens were captured.

Plot	Rating	No. sites with rating	Observed captures	Expected captures
Marsh #3[a]	1	0	--	-
	2	0	--	-
	3	13	0	4.0
	4	12	0	3.7
	5	24	15	7.4

[a]Significant difference, $\chi^2 = 15.49$, $\underline{P} < 0.005$.

General Vegetative Structure

When each of the four community types investigated was characterized by their general physiognomy (Elton and Miller 1954), essentially two structural types were evident, each with a characteristic small mammal fauna. One type consisted of the 10 plots in the sagebrush or greasewood shrub vegetation. This type had relatively few plant species but a relatively large degree of structural diversity. The other physiognomic type, which consisted of the eight plots in marsh or grassland areas, was characterized by a large number of plant species, at least in grassland areas, but a generally low degree of structural diversity (Fig. 10).

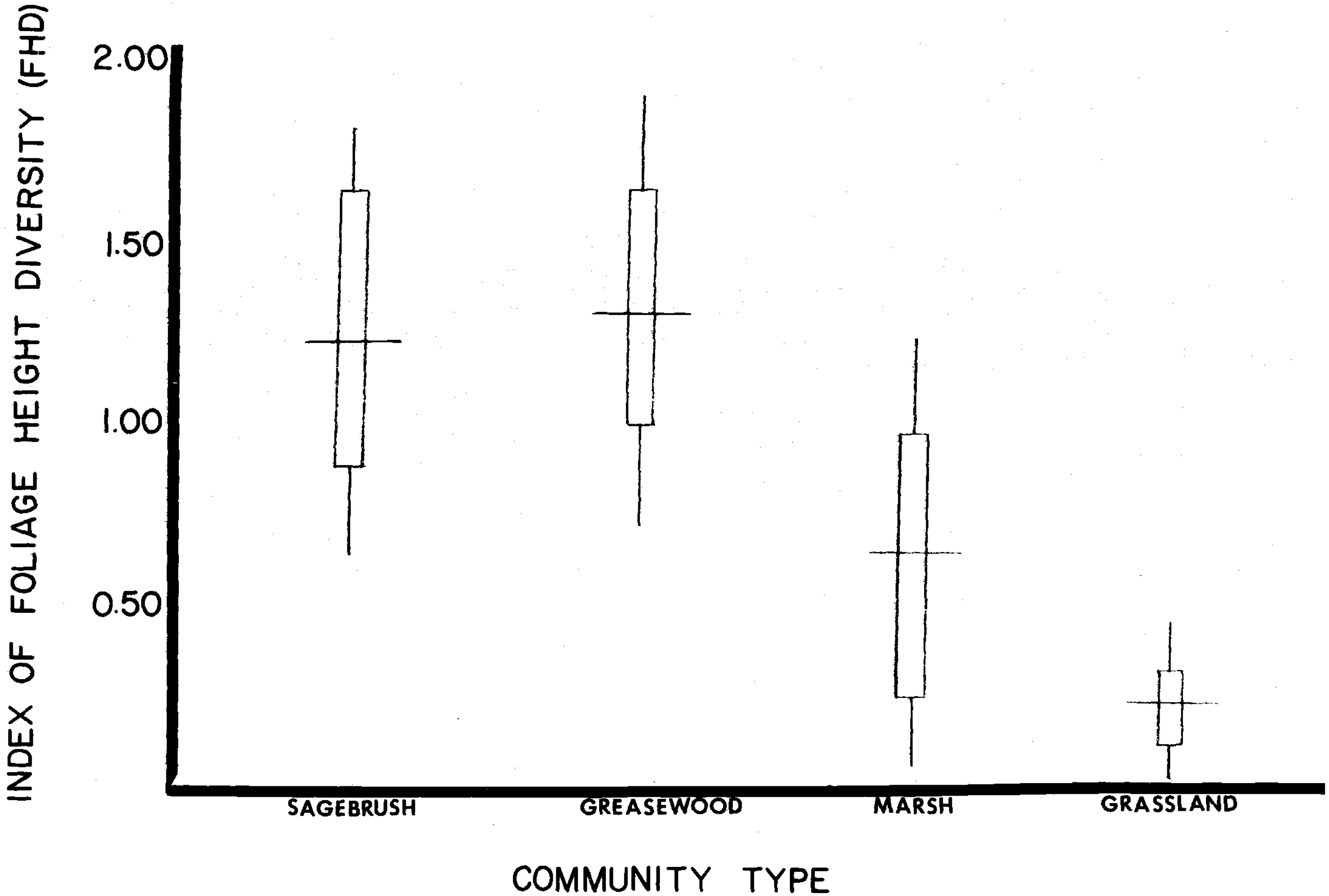


Figure 10. Mean (horizontal line), standard deviation (vertical line) and range (rectangle) for the index values of foliage height diversity of study plots in each habitat type during the initial trapping period of 1974 on Malheur National Wildlife Refuge.

The effect of foliage structure on the distribution of species of small mammals was evident in this study. With the exception of deer mice, each species of small mammal was restricted to one of the two physiognomic types. The small mammal fauna associated with the sagebrush-greasewood type was relatively diverse. It included the four species of heteromyids captured, the only species of chipmunk found on the refuge, and five other rodent species (Table 1). Voles, western harvest mice (Reithrodontomys megalotis) and shrews (Sorex vagrans) were restricted to the marsh-grassland physiognomic type. Although the small mammal fauna was not as diverse, larger population densities were encountered in this type. It should be noted that voles and harvest mice were not considered residents in greasewood areas. All individuals of these species captured in greasewood habitat were found on plot no. 5. These 20 individuals were captured while a fire smoldered in dry marsh vegetation 40 m from the plot during September 1974. Presumably these conditions forced voles and harvest mice from their preferred habitat, as neither of these species were captured on plot no. 5 during the two trapping periods prior to the fire. Dice (1931) first suggested that the physiognomy of the vegetation was an important factor in the local distribution of animal species. Since then, this generalization has been corroborated with regard to many species of small mammals (Hardy 1945, Fautin 1946, Pearson 1959, Tester and Marshall 1961, Allred and Beck 1963, M'Closkey and Lajoie 1975).

Interspecific Competition

Evidence of interspecific competition may include "two sympatric species which exhibit an inverse numerical relationship" (Grant 1972:79). Competitive interaction, in terms of inverse numerical relationships, was examined with regard to the populations of small mammals in each habitat type by linear regression analysis. Both the estimated ("absolute") density and the proportional representation ("relative density") of each species in the small mammal fauna were considered.

In greasewood habitat, an inverse relationship was apparent between the absolute densities of chipmunks and pocket mice ($r^2 = 0.54$, $\underline{P} < 0.005$), and between their relative densities ($r^2 = 0.57$, $\underline{P} < 0.005$). In sagebrush habitat, an inverse correlation was evident between the relative densities of chipmunks and deer mice ($r^2 = 0.32$, $\underline{P} < 0.05$). With regard to the evidence noted above, competition between these species was suggested.

A statistically significant direct correlation between the absolute densities of deer mice and pocket mice was evident on the greasewood plots ($r^2 = 0.22$, $\underline{P} < 0.05$), although not in sagebrush. In both habitat types: 1) pocket mice generally began breeding about 1 month later than deer mice; 2) the greatest numbers of juvenile pocket mice were found during July, and corresponded with the fewest numbers of juvenile deer mice; 3) peak reproductive activity of deer mice occurred both before and after that of pocket mice; and 4) the dispersion of each species in relation to cover was different. Similar reproductive and microhabitat findings, and differences in diet, let Kritzman (1974) and O'Farrell (1975) to conclude that direct competition probably does not occur between these species. If individuals of both species had very broadly overlapping niches, however, population densities of each species could exhibit similar changes in response to variable resource availability. Although competition may have occurred under these conditions, it would not have been apparent. Differences in diet, reproductive and microhabitat factors may actually have been the result of character displacement (Miller 1967, Emlen 1973).

No numerical relationships existed between population densities of deer mice and montane voles in the marsh areas. Although exceptions have been reported (Grant 1971), the lack of numerical relationship was consistent with previous conclusions regarding the probable absence of interspecific competition between species of these genera (Getz 1961, M'Closkey 1975, M'Closkey and Lajoie 1975).

Therefore, considering only inverse numerical relationships, an apparent competitive interaction was evident only between chipmunks and the other two species of small mammals common on sagebrush and greasewood areas. Although these results were suggestive, this study was not designed to quantify the degree of niche overlap between species. The possibility remained that the inverse numerical relationships observed were the result of ecological differences between each species with regard to factors of the habitats (Miller 1967, Grant 1972).

Possible Effects of Certain Land-Use Practices on the Small Mammal Fauna

Land-use practices may not always change the climax state of a community, although they may alter some of the physiognomic aspects (Tester and Marshall 1961). These aspects may in turn impinge upon the small mammal fauna in the community. Practices that may have effected changes in population densities of small mammals on the study plots included mowing and removal of vegetation, and grazing by livestock.

Mowing and Livestock Grazing--Both these practices produced similar changes in the vegetation. Mowing occurred primarily on grassland areas. It greatly reduced or eliminated populations of voles (see p. 50), the predominant species of small mammal in grassland habitat, because it reduced foliage cover and altered the vegetative profile.

Livestock grazed in all four community types investigated. On the shrub areas, grazing reduced the amount of perennial grass cover and increased the abundance of cheat grass, and although sagebrush coverage is not actually affected by past grazing, greasewood apparently is (Daubenmire 1970). Although no relationship between the population densities of deer mice or chipmunks and vegetative cover was apparent in this study, depletion of shrub vegetation was cited as a causitive factor in the increased population densities of these species (Larrison and Johnson 1973), as well as Ord's Kangaroo rat (Dipodomys ordii) (McCulloch 1962). As noted, however, population densities of Great Basin pocket mice were directly associated with cover, and were probably reduced by excessive livestock grazing (Larrison and Johnson 1973). Therefore, no generalizations could be made.

Neither could generalizations be made regarding the effect on specific rodent species of livestock grazing in the marsh and grassland communities. Diminished cover adversely affected the density of vole populations, but may have enhanced population densities of deer mice. Deer mice, however, represented only 13.6 percent of the rodents captured in marsh areas and only 0.8 percent of those captured in grassland. Voles represented 76.2 percent and 82.0 percent of the small mammals, respectively, captured in each habitat type. Therefore, the total abundance of the small mammal fauna was generally lower on grazed than on ungrazed areas in marsh and grassland habitat types (Howard 1953, Pefaur and Hoffmann 1975), and probably increased with the degree of grazing on shrub areas (Norris 1950).

CONCLUSIONS AND RECOMMENDATIONS

Consideration of apparent relationships between vegetative and edaphic factors and populations of the common species of small mammals on the refuge suggested possible management alternatives. Unless measures are applied directly to the animals themselves, management of rodent species must be based primarily on manipulation of vegetative factors, because manipulation of most edaphic components of the habitat is generally impractical.

On the basis of the results of this research, the following conclusions and management recommendations are made:

1) Because Great Basin pocket mice attained their greatest densities in areas dominated by sagebrush, enhancement of this shrub, especially on soils with a high sand fraction in the A horizon, probably would increase densities of pocket mice. Eradication of sagebrush, or severe reduction of the cover on these areas, probably would reduce population densities of pocket mice.

2) Reducing the amount of area dominated by greasewood, marsh or grassland, and replacement of these types of vegetation by sagebrush, probably would increase densities of Great Basin pocket mice.

3) Increasing the amount of area dominated by greasewood, marsh or grassland might reduce population densities of pocket mice.

4) Increasing the amount of area dominated by greasewood, especially on soils with a high clay fraction in the A horizon, might increase population densities of least chipmunks.

5) Increased cover is apparently of minor importance to least chipmunks, and light to moderate reduction of shrub cover may increase population densities of this species.

6) Eradication of greasewood and sagebrush vegetation probably would result in severe reduction or elimination of populations of chipmunks.

7) Because deer mice were most abundant in greasewood areas with soils of high clay fraction, and in marsh areas of high sand fraction, increasing the amount of area with these features probably would increase population densities of deer mice.

8) Light to moderate reduction of cover in greasewood and marsh areas, as well as in areas dominated by sagebrush, probably would increase population densities of deer mice.

9) Reduced population densities of deer mice might result from increasing the amount of area dominated by sagebrush or grass vegetation, especially in those areas with a high

fraction of sand in the A horizon of the soil. Eradication of greasewood or marsh vegetation also would tend to reduce or eliminate population densities of deer mice.

10) Increased vegetative cover or continuity of cover in marsh and grassland habitats appeared to be a necessary prerequisite for increased densities of montane voles.

11) Severe reduction of cover, by mowing for example, has the immediate effect of decreasing or eliminating population densities of voles. Considering their high potential for reproduction and dispersal, however, this is undoubtedly a short-term effect. Immigration probably occurs concurrently with suitable regrowth of the vegetation. Therefore, periodic reduction or elimination of the vegetation, perhaps at 3-month intervals or when the mean amount of cover equals about 40 percent, essentially would eliminate voles. Only twice were montane voles trapped in marsh or grassland habitats with less than 40 percent vegetative cover.

12) In general, reducing the structural diversity of the vegetation on areas dominated by sagebrush and greasewood probably would reduce the diversity of the small mammals in those areas, although subsequent densities probably would remain close to the initial values.

13) Management practices that reduced densities of voles in areas dominated by marsh and grassland habitats may eventually increase the diversity of the small mammal fauna slightly, although absolute densities of small mammals probably would remain below the initial levels.

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APPENDICES

Table A. The location and description of the 18 study plots on Malheur National Wildlife Refuge and inclusive trapping dates for small mammals.

Plot	Location	Soil texture	$\bar{x}$ Soil sheer-stress (kg/cm^2)	$\bar{x}$ Soil depth (cm)	$\bar{x}$ % Soil moisture	$\bar{x}$ % Vegetative cover	Dominant plants with % of total cover	Trapping dates
(Sagebrush)								
1	T26S, R31E, NW 1/4 Sec. 28	sandy-loam	1.4	97.3	6.1	30.9	*Artemisia tridentata* (65.0) *Sarcobatus vermiculatus* (32.0)	14-17 July 1973; 22-June-2 July 1974; 20-29 August 1974; 25 April-4 May 1975
2	T27S, R30E, SE 1/4 Sec. 25	sandy-loam	1.8	>101.6	10.4	42.6	*Artemisia tridentata* (77.2) *Atriplex confertifolia* (16.9) *Sarcobatus vermiculatus* (5.4)	10-13 Aug. 1973; 7-16 July 1974; 27 Sept. -6 Oct. 1974; 26 May-4 June 1975
3	T27S, R31E, SW 1/4 Sec. 14	clay-loam	1.0	50.5	11.2	33.8	*Artemisia tridentata* (85.4) *Grayia spinosa* (9.5)	10-13 Aug. 1973; 7-16 July 1974; 27 Sept. -6 Oct. 1974; 26 May-4 June 1975
4	T29S, R31E, SW 1/4 Sec. 35	sandy-loam-clay	0.9	33.8	9.1	22.7	*Artemisia tridentata* (82.8) *Sarcobatus vermiculatus* (10.5)	8-10 Sept. 1973; 23 July-1 Aug. 1974; 14-23 Oct. 1974; 9-18 May 1975
5	T31S, R32 1/2E, SW 1/4 Sec. 33	loam	0.5	30.7	7.4	29.9	*Artemisia tridentata* (70.0) *Sarcobatus vermiculatus* (26.4)	15-17 Sept. 1973; 5-14 Aug. 1974; 3-12 Nov. 1974; 26 May-4 June 1975

Table A. Continued.

Plot	Location	Soil Texture	$\bar{x}$ Soil sheer-stress (kg/cm^2)	$\bar{x}$ Soil depth (cm)	$\bar{x}$ % Soil moisture	$\bar{x}$ % Vegetative cover	Dominant plants with % of total cover	Trapping dates
(Greasewood)								
1	T26S, R30E, NW 1/4 Sec. 30	sandy-loam	1.0	>101.6	5.4	25.8	Sarcobatus vermiculatus (84.9) Atriplex confertifolia (6.3)	14-17 July 1973; 22 June-2 July 1974; 20-29 Aug. 1974; 25 April-4 May 1975
2	T27S, R31E, SW 1/4 Sec. 32	clay	1.2	>101.6	29.2	63.9	Sarcobatus vermiculatus (99.2)	28-31 Aug. 1973; 7-16 July 1974; 27 Sept. -6 Oct. 1974
3	T28S, R31E, SW 1/4 Sec. 5	clay-loam	2.4	>101.6	24.8	51.8	Sarcobatus vermiculatus (34.9) Chrysothamnus visidiflorus (34.9) Elymus cinereus (19.6)	28-31 Aug. 1973; 7-16 July 1974; 27 Sept. -6 Oct. 1974; 26 May-4 June 1975
4	T28S, R31E, SW 1/4 Sec. 35	clay	1.8	95.2	13.1	21.4	Sarcobatus vermiculatus (58.9) Artemisia tridentata (38.4)	8-10 Sept. 1973; 23 July-1 Aug. 1974; 14-23 Oct. 1974; 9-18 May 1975
5	T30S, R31E, SE 1/4 Sec. 27	sandy-clay-loam	0.2	40.9	7.8	35.5	Sarcobatus vermiculatus (54.4) Grayia spinosa (40.4)	8-10 Sept. 1973; 5-14 Aug. 1974; 3-12 Nov. 1974; 9-18 May 1975
(Marsh)								
1	T26S, R28E, SE 1/4 Sec. 24	clay-loam	4.0	>101.6	32.4	34.8	Scirpus paludosus (62.4) Eleocharis palustrus (37.6)	14-17 July 1973; 22 June-2 July 1974; 20-29 Aug. 1974

Table A. Continued.

Plot	Location	Soil texture	$\bar{x}$ Soil sheer-stress (kg/cm^2)	$\bar{x}$ Soil depth (cm)	$\bar{x}$ % Soil moisture	$\bar{x}$ % Vegetative cover	Dominant plants with % of total cover	Trapping dates
2	T26S, R32E, SW 1/4 Sec. 32	clay-loam	1.7	> 101.6	50.5	41.2	*Eleocharis palustrus* (100.0)	22 June-2 July 1974; 20-29 Aug. 1974; 25 April-4 May 1975
3	T29S, R31E, NW 1/4 Sec. 11	clay	0.3	> 101.6	65.1	86.4*	*Sparganium* sp. (88.1) *Typha latifolia* (5.0)	28-31 Aug. 1973; 23 July-1 Aug. 1974; 14-23 Oct. 1974; 9-18 May 1975
4	T30S, R31E SW1/4 Sec. 34	clay	0.0	> 101.6	95.3	95.6	*Sparganium* sp. (100.0)	15-17 Sept. 1973; 5-14 Aug. 1974; 3-12 Nov. 1974
(Grassland)								
1	T26S, R31E SW 1/4 Sec. 25	silt-loam	1.0	94.5	49.4	55.5*	*Poa* sp. (62.2) *Eleocharis palustrus*, *Spartina gracilis*, *Hordeum jubatum*, *Aster* sp. (8.0)	10-13 Aug, 1973; 22 June-2 July 1974; 20-29 Aug. 1974; 25 April-4 May 1975
2	T30S, R32E, SE 1/4 Sec. 18	clay	1.3	> 101.6	33.5	77.4*	*Agropyron smithii* (94.1) *Juncus balticus*, *Hordeum jubatum*, *Puccinellia* sp. (5.6)	8-10 Sept. 1973; 23 July-1 Aug. 1974; 14-23 Oct. 1974

Table A. Continued.

Plot	Location	Soil texture	$\bar{x}$ Soil sheer-stress (kg/cm^2)	$\bar{x}$ Soil depth (cm)	$\bar{x}$ % Soil moisture	$\bar{x}$ % Vegetative cover	Dominant plants with % of total cover	Trapping dates
3	T31S, R32 1/2 E, SW 1/4 Sec. 18	--	1.4	>101.6	24.0	89.5	*Distichlis stricta* (45.0) *Juncus balticus* (25.0) *Carex* sp. (8.0)	5-14 Aug. 1974; 3-12 Nov. 1974
4	T32S, R32 1/2 E, SW 1/4 Sec. 6	--	1.1	>101.6	28.0	85.4*	*Carex* sp. (24.0) *Poa secunda* (20.0) *Distichlis stricta* (12.0) *Muhlenbergia asperifolia* (12.0) *Elymus triticoides* } (7.0) *Juncus balticus* }	5-14 Aug. 1974; 3-12 Nov. 1974

*Excludes a trapping period on plot when vegetation was mowed.

Table B. Mammalian, avian and reptilian predators that may have utilized the small mammal fauna inhabiting the 18 study plots on Malheur National Wildlife Refuge during the study. Avian species include those which occur at least "occasionally" during one season of the year.

Class	Predator
Mammalia	Coyote (Canis latrans)
	Bobcat (Lynx rufus)
	Long-tailed Weasel (Mustela frenata)
	Mink (Mustela vison)
	Badger (Taxidea taxus)
	Spotted Skunk (Spilogale putorious)
	Striped Skunk (Mephitis mephitis)
Aves	Goshawk (Accipiter gentilis)
	Cooper's Hawk (A. cooperi)
	Sharp-shinned Hawk (A. striatus)
	Rough-legged Hawk (Buteo lagopus)
	Ferruginous Hawk (B. regalis)
	Red-tailed Hawk (B. jamaicensis)
	Swainson's Hawk (B. swainsoni)
	Golden Eagle (Aquila chrysaetos)
	Prairie Falcon (Falco mexicanus)
	Merlin (F. columbarius)
	American Kestrel (F. sperverius)
	Marsh Hawk (Circus cyaneus)
	Great Horned Owl (Bubo virginianus)
	Long-eared Owl (Asio otus)
	Short-eared Owl (A. flammeus)
	Burrowing Owl (Speotyto cunicularia)
Reptilia	Great Basin Rattlesnake (Crotalus viridus)
	Great Basin Gopher Snake (Pituophis melanoleucus)
	Western Yellow bellied Racer (Coluber constrictor)
	Desert Night Snake (Hypsiglena torquata)
	Valley Garter Snake (Thamnophis sirtalis)
	Striped Whipsnake (Masticophis taeniatus)

Table C. Estimated population densities, standard deviation and coefficient of variation for three species of small mammals common on study plots in sagebrush communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

		Density small mammal species/plot (1. 1 ha)								
		P. maniculatus			P. parvus			E. minimus		
Period	Plot	$\bar{N}$	SD	CV(100)	$\bar{N}$	SD	CV(100)	$\bar{N}$	SD	CV(100)
1	1	4.8	0.38	8.	5.5	0.96	17.	7.7	3.18	41.
	2	13.7	2.37	17.	5.5	0.50	9.	2.3	0.33	14.
	3	2.3	0.33	14.	8.4	0.44	5.	2.0	0.57	29.
	4	1.0	0.00	--	9.0	2.02	22.	0.0	--	--
	5	3.2	0.25	8.	9.5	1.50	16.	0.0	--	--
2	1	2.8	0.40	14.	9.3	0.94	10.	7.9	1.12	14.
	2	6.9	0.52	8.	12.5	1.43	11.	9.7	1.59	16.
	3	0.8	0.27	34.	5.8	0.81	14.	3.6	0.41	11.
	4	0.8	0.14	18.	6.0	0.49	8.	0.0	--	--
	5	2.9	0.14	5.	4.4	0.67	15.	0.0	--	--
3	1	6.3	0.46	7.	15.1	2.59	17.	6.4	0.56	9.
	2	5.7	0.34	6.	11.6	1.64	14.	9.4	0.73	8.
	3	3.0	0.00	--	5.4	0.22	4.	5.9	0.73	12.
	4	8.5	1.64	19.	5.0	0.25	5.	0.0	--	--
	5	24.4	3.38	14.	6.7	0.33	5.	0.0	--	--
4	1	0.8	0.14	18.	10.8	0.89	8.	13.9	1.04	7.
	2	2.9	0.28	10.	16.3	0.65	8.	6.0	0.60	10.
	3	3.0	0.28	9.	4.8	0.15	3.	2.2	0.45	20.
	4	14.8	0.83	6.	12.0	0.75	6.	0.0	--	--
	5	11.8	0.98	8.	12.3	0.31	3.	0.0	--	--

Table D. Estimated population densities, standard deviation and coefficient of variation for three species of small mammals common on study plots in greasewood communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

		Density/plot (1.1 ha)								
		P. maniculatus			P. parvus			E. minimus		
Period	Plot	$\bar{N}$	SD	CV(100)	$\bar{N}$	SD	CV(100)	$\bar{N}$	SD	CV(100)
1	1	9.3	2.03	22.	8.7	2.67	31.	1.7	0.67	39.
	2	9.2	1.97	21.	0.0	--	--	16.9	1.73	10.
	3	6.2	1.15	18.	0.7	0.72	103.	6.5	2.60	40.
	4	2.0	1.0	50.	0.0	--	--	14.3	0.30	2.
	5	5.3	0.33	6.	2.0	0.00	--	0.0	--	--
2	1	6.5	0.98	15.	8.3	0.98	12.	2.1	0.69	33.
	2	10.1	1.77	17.	0.0	--	--	9.8	0.87	9.
	3	9.1	0.71	8.	1.3	0.17	13.	10.7	1.55	14.
	4	4.4	0.40	9.	0.0	--	--	9.8	0.48	5.
	5	4.4	0.51	12.	4.0	0.31	8.	0.0	--	--
3	1	7.2	0.41	6.	11.9	0.85	7.	5.1	0.81	16.
	2	20.1	1.69	8.	0.0	--	--	13.6	2.27	17.
	3	17.0	0.99	6.	1.8	0.15	8.	6.6	0.83	13.
	4	7.8	0.87	11.	1.0	0.00	--	11.6	1.23	11.
	5	4.3	0.86	20.	0.7	0.02	2.	0.0	--	--
4	1	3.5	0.46	13.	3.4	0.29	9.	5.9	0.69	12.
	2		a			a			a	
	3	18.2	1.12	6.	8.7	0.29	3.	4.4	0.52	12.
	4	15.0	0.89	6.	3.9	0.77	20.	3.5	0.35	10.
	5	20.5	1.97	10.	10.7	0.68	6.	0.0	--	--

[a] Plot flooded, could not be operated.

Table E. Percentage fractions of sand, silt and clay and associated soil texture classifications for study plots on Malheur National Wildlife Refuge from July 1973 through June 1975.

Community	Plot	% Sand	% Silt	% Clay	Classification[a]
Sagebrush	1	65.5	20.2	14.3	sandy-loam
	2	40.8	31.4	27.8	clay-loam-loam
	3	51.6	32.9	15.5	sandy-loam
	4	53.6	16.2	31.2	sandy-clay-loam
	5	47.7	30.9	21.4	loam
Greasewood	1	74.0	12.8	13.2	sandy-loam
	2	14.7	33.8	51.5	clay
	3	24.0	37.8	38.2	clay-loam
	4	41.6	14.2	44.2	clay
	5	53.9	20.6	25.5	sandy-clay-loam
Marsh	1	35.0	26.8	38.2	clay-loam
	2	24.7	42.6	32.7	clay-loam
	3	24.5	17.9	57.6	clay
	4	19.6	15.6	66.8	clay
Grassland	1	25.3	61.2	13.5	silt-loam
	2	18.5	32.9	48.6	clay
	3	--	--	--	--
	4	--	--	--	--

[a]From Dawson (1972).

Table F. Mean percentage of soil moisture each trapping period on study plots on Malheur National Wildlife Refuge from July 1973 through June 1975.

Community	Plot	Trapping Period 1	2	3	4
Sagebrush	1	2.2	4.9	4.9	12.5
	2	6.6	14.9	11.3	8.4
	3	6.9	13.9	12.0	12.2
	4	5.5	8.9	7.2	14.7
	5	5.0	5.7	6.8	12.0
Greasewood	1	2.2	5.6	5.1	8.9
	2	23.8	37.4	26.3	a
	3	19.4	25.8	21.0	33.2
	4	12.5	11.0	11.2	17.9
	5	4.2	5.6	6.1	14.0
Marsh	1	25.4	43.3	28.5	a
	2	--	55.8	35.6	60.0
	3	50.4	84.4	41.9	83.7
	4	91.6	86.5	107.8	a
Grassland	1	69.7	60.3	56.4	59.6
	2	34.2	37.5	28.9	a
	3	--	23.0	25.1	a
	4	--	32.2	23.7	a

[a]Plot flooded, could not be operated.

Table G. Mean percentage vegetative moisture (succulence) on study plots during the final three trapping periods on Malheur National Wildlife Refuge, June 1974 through June 1975.

Period	Plot	Community type: Sagebrush	Greasewood	Marsh	Grassland
2	1	182.1	209.7	187.4	223.4
	2	140.0	402.1	329.4	192.4
	3	117.5	298.1	474.9	154.8
	4	92.8	316.6	283.7	164.5
	5	102.6	211.1	---	---
3	1	96.8	275.2	302.3	121.2
	2	74.9	52.3	248.6	6.7
	3	42.1	160.5	23.3	10.0
	4	73.3	43.9	18.8	45.4
	5	42.8	22.7	---	---
4	1	293.0	71.4[b]	c	23.4
	2	228.8	b	20.4	c
	3	222.0	448.4	159.0	c
	4	297.4	582.9	c	c
	5	246.2	303.7	---	---

[a]This factor was not determined during the initial trapping period.

[b]Greasewood had not yet bloomed.

[c]Plot flooded, could not be operated.

Table H. Index of foliage height diversity (FHD) and proportion of vegetation in each layer (P_i) for study plots in each community type during the initial trapping period of 1974 on Malheur National Wildlife Refuge.

Community	Plot	FHD	P_1	P_2	P_3
Sagebrush	1	1.44	.531	.328	.141
	2	1.29	.541	.372	.086
	3	1.62	.464	.375	.161
	4	0.89	.688	.216	.096
	5	0.97	.668	.211	.120
Greasewood	1	1.19	.583	.329	.088
	2	1.06	.643	.250	.106
	3	1.61	.461	.382	.157
	4	1.69	.485	.303	.212
	5	1.01	.656	.236	.107
Marsh	1	1.00	.646	.276	.078
	2	0.30	.868	.132	.000
	3	0.59	.776	.149	.075
	4	0.82	.715	.176	.109
Grassland	1	0.12	.930	.060	.010
	2	0.35	.850	.120	.040
	3	0.33	.850	.120	.020
	4	0.35	.850	.140	.010

Table I. Estimated population densities, standard deviation and coefficients of variation for two species of small mammals common on study plots in marsh communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

		Density/Plot (1.1 ha)					
		P. maniculatus			*M. montanus*		
Period	Plot	$\bar{N}$	SD	CV(100)	$\bar{N}$	SD	CV(100)
1	1	5.6	0.91	16.	0.0	--	--
	2	trapping not conducted on plot					
	3	0.0	--	--	169.5	30.0	18.
	4	0.0	--	--	252.8	82.2	33.
2	1	5.2	1.04	20.	0.0	--	--
	2	0.0	--	--	0.0	--	--
	3	4.7	0.80	17.	46.6	5.4	14.
	4	1.3	0.55	43.	36.5	4.7	13.
3	1	8.2	1.07	13.	0.0	--	--
	2	0.0	--	--	0.1	--	--
	3	6.4	0.48	7.	33.9	6.7	20.
	4	5.4	1.58	29.	40.2	13.9	35.
4	1		a			a	
	2	0.0	--	--	0.0	--	--
	3	1.4	0.24	17.	4.2	0.8	19.
	4		a			a	

[a] Plot was flooded and could not be operated.

Table J. Mean percentage vegetative cover on study plots on Malheur National Wildlife Refuge from June 1974 through June 1975. Associated "patchiness" of cover is in parentheses.[a]

Community	Plot	Trapping period 1	2	3	4
Sagebrush	1	25.8	31.3 (2.12)	43.4 (3.17)	23.2 (1.38)
	2	40.8	33.3 (1.38)	38.3 (2.57)	58.0 (2.33)
	3	31.6	42.5 (2.85)	32.6 (2.12)	28.8 (1.38)
	4	23.8	19.1 (0.85)	27.9 (1.94)	20.2 (1.17)
	5	20.8	36.5 (3.17)	34.9 (1.63)	27.2 (0.92)
Greasewood	1	15.9	32.0 (1.63)	38.0 (2.33)	17.4 (1.27)
	2	67.5	63.6 (2.57)	60.7 (1.30)	b
	3	68.7	64.2 (2.33)	33.4 (2.57)	41.1 (2.33)
	4	19.5	16.2 (0.52)	26.8 (1.78)	22.9 (0.85)
	5	28.5	41.2 (3.55)	50.7 (1.94)	21.7 (0.72)
Marsh	1	35.0	30.3 (1.63)	39.0 (2.33)	b
	2	--	23.0 (1.17)	62.4 (1.27)	38.2 (2.33)
	3	98.0	91.7 (0.22)	79.4 (0.85)	78.3 (1.17)
	4	99.0	93.4 (0.00)	94.6 (0.00)	b
Grassland	1	18.4	63.0 (1.38)	72.3 (1.38)	30.2 (2.12)
	2	85.0	69.8 (1.27)	43.3 (1.94)	b
	3	--	87.2 (0.22)	91.9 (0.22)	b
	4	--	85.4 (0.22)	25.3 (1.38)	b

[a]Patchiness was not determined during the initial trapping period.

[b]Plot flooded, could not be operated.

Table K. Estimated population densities, standard deviation and coefficient of variation for montane voles on study plots in grassland communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

		Density/Plot (1.1 ha) *M. montanus*		
Period	Plot	$\bar{N}$	SD	CV(100)
1	1	3.3	0.88	27.
	2	2.0	1.00	50.
	3	trapping not conducted on plot		
	4	trapping not conducted on plot		
2	1	0.0	--	--
	2	0.0	--	--
	3	19.1	4.26	22.
	4	15.4	1.82	12.
3	1	2.2	0.40	18.
	2	0.0	--	--
	3	20.3	3.94	19.
	4	0.1	--	--
4	1	0.0	--	--
	2		a	
	3		a	
	4		a	

[a]Plot flooded, could not be operated.

Table L. Mean soil depth and soil sheer stress (strength) values, with associated diversity indices, for study plots on Malheur National Wildlife Refuge during the initial trapping period of 1974.

Community	Plot	Mean Soil Depth (cm)	Diversity	Mean Sheer Stress (Kg/cm^2)	Diversity
Sagebrush	1	97.3	0.22	1.4	1.17
	2	101.6+	0.00	1.8	1.17
	3	50.5	2.57	1.0	0.92
	4	33.8	0.92	0.9	0.47
	5	30.7	1.63	0.5	0.22
Greasewood	1	101.6+	0.00	1.0	0.72
	2	101.6+	0.00	1.2	0.85
	3	101.6+	0.00	2.4	2.33
	4	95.2	0.22	1.8	0.52
	5	40.9	0.52	0.2	0.00
Marsh	1	101.6+	0.00	4.0	0.47
	2	101.6+	0.00	1.7	1.78
	3	101.6+	0.00	0.3	0.00
	4	101.6+	0.00	0.0	0.00
Grassland	1	94.5	0.00	1.0	0.47
	2	101.6+	0.00	1.3	0.47
	3	101.6+	0.00	1.4	0.72
	4	101.6+	0.00	1.1	0.92

Table M. Summary of statistically significant relationships between mean population densities of the four common species of small mammals and habitat factors in communities where resident populations occurred.[a]

Habitat factor	*P. maniculatus* Sage	*P. maniculatus* Grease	*P. maniculatus* Marsh	*P. parvus* Sage	*P. parvus* Grease	*E. minimus* Sage	*E. minimus* Grease	*M. montanus* Marsh	*M. montanus* Grass
Mean density deer mice					*	*			
Mean density pocket mice		*					***		
Mean density chipmunks	*				***				
% Soil moisture		***							
Mean sheer stress				***		*	*		
Sheer stress diversity				*		***			
Mean soil depth				*		***			
Soil depth diversity				**					
% Sand		**	*		*				
% Clay				*			*		
Mean vegetative succulence									
Mean % cover								***	**
Patchiness of cover								***	***
Foliage height diversity									
Proportion vegetation below 15 cm									
Proportion vegetation between 15 and 46 cm						*			
Proportion vegetation above 46 cm									
Total vegetation in $q_{1,3.5}$	***	**							
Proportion vegetation above 7.6 cm									
Proportion vegetation above 15 cm									
Proportion vegetation above 30 cm									
Proportion vegetation above 46 cm									
Lag effects		succulence of veg.; soil moisture		succulence of veg.		soil strength; strength-diversity; P_1, P_2	succulence of veg.	cover; patchiness of cover	

[a]* Significant at $P < 0.05$; ** $P < 0.025$; *** $P < 0.01$ or less, during at least one season of the year.